

The South American Gracile Mouse Opossums, Genus *Gracilinanus* Gardner and Creighton, 1989 (Marmosidae, Marsupialia): A Taxonomic Review with Notes on General Morphology and Relationships

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Abstract

Gracile mouse opossums, genus *Gracilinanus*, are described and compared to other marsupials. Nine species are recognized, three of them described as new; subspecies are not considered. As setting for the descriptions and discussions, extant genera of mouse opossums are arranged within five subfamilies of the family Marmosidae (new), as follows: Marmosinae (new), Thylamyinae (new), Lestodelphyinae (new), Monodelphinae (new rank), and Metachirinae (new rank). The Marmosinae, represented by the genera *Gracilinanus*, *Marmosa*, *Marmosops*, and *Micoureus*, are pouchless, prehensile-tailed didelphoids with chromosome complements $2n = 14$ and 22 . Diagnostic keys are offered to the identification of these and other subfamilies and genera of the Marmosidae. Characters discussed include body size, tail, unguis, mammae, sex ratios, tympanic bullae, palate, dental formulae, thoracolumbar flexure, and tarsal bones.

Introduction

The Marmosinae or true murine opossums of the family Marmosidae include some of the smallest, most primitive, most diversified, and among the least understood living American opossums. Next to those of the genus *Didelphis*, they are the most abundant and widespread of living New World marsupials (fig. 1). The approximately 45 species of marmosine opossums, distributed among the genera *Gracilinanus*, *Marmosops*, *Marmosa*, and *Micoureus*, are confined to wooded parts of the Neotropical region from sea level to about 4500 m, the highest elevations inhabited by New World sylvan mammals.

Marmosine opossums or nearest marmosid relatives can be traced to the North American Cretaceous or to the earliest known metatherians (Hershkovitz, 1982, in prep.). All living forms are similar in general appearance: they are pouchless

and prehensile-tailed, and their ankle bones are specialized. Principal differentiations appear to have involved body size, color, pelage, postcranial skeleton, reproductive systems, volar pads, caudal hairs and scales, and a trend toward reduction in litter size indicated by reduction in the number of teats. Overall, mouse opossums have been endowed with the adaptability and fecundity that would ensure their survival over a period of time that may be the longest for any order of living New World mammals.

The present review of the cluster of murine opossums, previously known as the *Marmosa microtarsus* section of Tate (1933), now genus *Gracilinanus* Gardner and Creighton, is intended to serve as framework for the description of three new species of the group and provide background for future reviews of sister genera. *Gracilinanus* is here compared to other mouse opossums as well as to representatives of other taxa of New World marsupials.



FIG. 1. Map of South America showing *Gracilinanus* collecting localities. See the gazetteer in Appendix 2 for explanation of numbers.

Material

The present study of gracile mouse opossums, genus *Gracilinanus*, is based on 63 adults and 1 young representing seven of the nine recognized species, of which three are described as new. A tenth, apparently new, is a previously unrecorded juvenal. Two specimens, collected by me in Colombia, were loaned by the Smithsonian Institution, and the juvenal by the University of Kansas Museum of Zoology. All but two representatives of other living American and Australian marsupials used in this study are in the collections of the Field Museum. Of these, one, *Lestodelphys halli*, was loaned by the Museum of Vertebrate Zoology, University of California, and the other, a skeleton of *Lutreolina crassicaudata*, by the University of Wisconsin Zoological Museum.

Methods

Standard cranial and dental measurements used are shown in figure 17, external measurements are those of the collectors, and cranial morphology is depicted in figures 18 through 20. Length given for each postcranial bone mentioned in table 3 is the greatest distance between proximal and distal points.

In his revision of the genus *Marmosa*, encompassing all mouse opossums, Tate (1933, tables) used 31 measurements for external, cranial, and dental characters. Only 13 are used here for definition and comparisons of the recognized species of *Gracilinanus*. The larger number of Tate's measurements owe partly to the greater number of taxa he recognized and partly to many individually variable characters.

Abbreviations for teeth are i, c, pm, and m for incisor, canine, premolar, and molar, respectively. A superscript or subscript is used to indicate upper or lower teeth. When reference is to the same numbered upper and lower tooth, a single number is used for both.

Abbreviations used for institutions mentioned in the text and tables are as follows:

AMNH	American Museum of Natural History, New York
BM	British Museum (Natural History), London
FMNH	Field Museum of Natural History, Chicago

MVZUC	Museum of Vertebrate Zoology, University of California, Berkeley
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C.
UWZM	University of Wisconsin Zoological Museum, Madison, Wisconsin

Classification of Living New World Marsupials of the Order Didelphidia (Gray), Superfamily Didelphoidea (Gray)

Most recent arrangements of living New World marsupials recognize three orders or suborders of living New World marsupials (Creighton, 1984; Reig et al., 1987; Marshall et al., 1990). These are (a) didelphoids of the order Didelphidia represented by 15 extant genera, of which 8 are now placed in the family Marmosidae (new), 2 in the family Caluromyidae, 1 in the family Glironiidae (new), and 4 in the family Didelphidae, (b) caenolestoids, order Paucituberculata, encompassing three living genera, all in the family Caenolestidae, and (c) microbiotherioids, order Microbiotheria, with the single extant genus *Dromiciops*, family Microbiotheriidae.

In the present classification, the pouchless mouse opossums, family Marmosidae, comprise the subfamilies Marmosinae or typical mouse opossums, with long, prehensile tails, short claws, and specialized ankle bones; Thylamyinae, with prehensile but incrassate tail, long, stout claws, parallel-sided nasal bones, unspecialized ankle bones, and extraordinarily large prostrate gland (fide Mann Fischer, 1978, p. 18), which may be seasonally variable only; the shrewlike Monodelphinae, with short nonprehensile tail, long claws, sagittally crested cranium, and unspecialized ankle bones; Lestodelphyinae, with short incrassate, nonprehensile tail, stout claws, sagittally crested skull, but specialized foot bones; and the outsize, terrestrial Metachirinae, with long nonprehensile tail and unspecialized foot bones. Salient diagnostic characters of the Marmosidae are summarized and those of the subfamilies and genera are keyed, discussed, and illustrated in the following pages. For a complete classification of American marsupials from cohort to species, see Hershkovitz (1992) and monograph in preparation.

- Class Mammalia Linnaeus, 1758
 Subclass Theria Parker and Haswell, 1897
 Infraclass Marsupialia Illiger, 1811
 Cohort Microbiotheriomorphia Ameghino, 1887
 Order Microbiotheria Ameghino, 1887
 Cohort Didelphimorphia Gill, 1872
 Order Didelphidia Gray, 1821
 Superfamily Didelphoidea Gray, 1821
 Family MARMOSIDAE (new)
 Subfamily Marmosinae (new)
Gracilinanus Gardner and Creighton, 1989
Marmosops Matschie, 1916
Marmosa Gray, 1821
Micoureus Lesson, 1842
 Subfamily Thylamyinae Reig, Kirsch, and Marshall, 1987, new rank
Thylamys Gray, 1843
 Subfamily Lestodelphyinae (new)
Lestodelphys Tate, 1934
 Subfamily Metachirinae Reig, Kirsch, and Marshall, 1987, new rank
Metachirus Burmeister, 1854
 Subfamily Monodelphinae (new)
Monodelphis Burnett, 1830
 Family Caluromyidae Kirsch and Reig, 1977
 Subfamily Caluromyinae Kirsch and Reig, 1977
Caluromys J. A. Allen, 1900
 Subfamily Caluromysiopsinae (new)
Caluromysiops Sanborn, 1951
 Family Glironiidae (new)
Glironia Thomas, 1910
 Family Didelphidae Gray, 1821
 Subfamily Didelphinae Gray, 1921
Philander Tiedmann, 1808
Didelphis Linnaeus, 1758
Chironectes Illiger, 1811
Lutreolina Thomas, 1910
 Subfamily uncertain
 Referred extinct genera (cf. Marshall et al., 1990, p. 481) known from fragmentary crania and molars

Note: The genus *Philander*, revised as part of the monograph in preparation, consists of the gray opossum *P. opossum* Linnaeus and the black opossum *P. andersoni* Osgood (= *P. mcilhennyi* Gardner and Patton).

Family Marmosidae: Diagnostic Characters

EXTERNAL—Marsupium absent; tail prehensile or not, seasonally incrassate or not, length more or less than head and body combined, base pilose like rump, remainder thinly or densely furred, scales showing through or not; fifth manual digit with sharp claw, hallux opposable, without unguis, toes slightly or not webbed; midfrontonasal stripe present or absent; paired whitish superciliary spots present or absent; teats 9–27 (reports of less [to 5] are miscounts); cloaca precaudal; glans penis usually bifid; length head and body combined, 70–310; tail, 45–390; greatest skull length, 22–68; habitat, all more or less wooded regions from Mexico south into Argentina and Chile.

CRANIAL—Skull light to moderately heavy; supraorbital region rounded, square, beaded or ridged; superior postorbital process absent or produced as short point or spine; inferior postorbital process often pointed, sometimes absent; temporal ridges present or absent, when present parallel-sided, bowed, or convergent to form low, thin sagittal crest; interparietal bone present; lambdoidal crest present or absent; palate vaulted, palatal vacuities variable, maxillopalatine pair always present; auditory bullae tripartite, with components alisphenoid, petrosal, and ectotympanic bones separate or touching but not fused.

POSTCRANIAL SKELETON—Vertebrae: 7 cervical; 12–13 thoracic; 5–7 lumbar; 2 sacral; 19–31 caudal including 4–6 transitional; paired articular facets of astragalus and calcaneus separate or continuous.

Dental: Adult, $i \begin{matrix} 1, 2, 3, 4, 5 \\ (1), 2, 3, 4, 5 \end{matrix}, c \begin{matrix} 1 \\ 1 \end{matrix}$,

$pm \begin{matrix} 1, 2, 3 \\ 1, 2, 3 \end{matrix}, m \begin{matrix} (1), 2, 3, 4, 5 \\ (1), 2, 3, 4, 5 \end{matrix} = \frac{13}{12}$.

Teeth lost in ontogeny or phylogeny are shown in parentheses; first upper and lower molars in juvenal are displaced by pm3 in adult.

Molars tritubercular, crowns dilambdomorphic (W-shaped) with well-developed buccal shelves; crowns of lower incisors touching, third (second in line) incisor staggered or crowded between adjacent teeth and buttressed by alveolar bone on buccal side; upper postcanine tooth rows divergent; first molar (m2) smaller than second; buccal shelf broad, distance between metacone and distostyle greater than distance between metacone and protocone; pm3 usually erupts before m5.

KARYOTYPES—Diploid number of chromosomes, 14, 18, and rarely 22.

Key to the Subfamilies and Genera of Pouchless Murine Opossums of the Family Marmosidae

Key characters given are of mature animals. Abbreviations for measurements of size are H&B, combined head and body length; T, tail length; and GSL, greatest skull length. Most cranial and tarsal characters mentioned below are discussed on pages 9–30; some are illustrated.

- I. Tail nonprehensile, shorter or longer than combined head and body length; manual claws weak or stout, protruding or not beyond terminal phalanges; throat gland present at least in males; karyotype $2n = 14, 18, \text{ or } 22$; bullar floor complete or with gap between petrous and alisphenoid components; superior border of frontal bone rounded, without postorbital process; lambdoidal crest well or poorly defined; low sagittal crest present at least in mature males; unworn, fully erupted third premolar larger than second, sometimes subequal.
 - A. Tail seasonally incrassate (fat storing) shorter than head and body combined, fully clothed, the hairs concealing scales; karyotype $2n = 14$; bullar floor complete, without gap, the ectotympanic, petrous, and alisphenoid components in contact but not fused, ectotympanic bone a wide band; zygomatic arch with large ascending postorbital process; paired articular facets of dorsal surface of calcaneus continuous; size, 2 ♂♂, H&B, 150, 132; T, 103, 88; GSL, 36.7, 35.4. Four specimens ex Marshall (1977), H&B, 132–144; T, 81–99; GSL, 31–33; habitat, S Argentina Lestodelphinae
 Sole genus: *Lestodelphys* Tate, 1934
 (monotypic, figs. 8–10; reviewed by Marshall, 1977)
 - B. Tail not incrassate longer or shorter than combined head and body, thinly clothed, the hairs not fully concealing scales; karyotype $2n = 14 \text{ or } 18$; bullar floor with gap between petrous and alisphenoid components, the tubular ectotympanic bone freely suspended between adjacent bones; zygomatic arch with or without weak ascending postorbital process; paired articular facets of dorsal surface of calcaneus separate.
 - 1. Karyotype $2n = 18$; tail shorter than head and body combined, moderately hirsute, the scales not fully concealed; superciliary spots absent; manual claws stout, extending well beyond terminal phalanges; pectoral teats present; weak ascending process of zygoma present; crowns of i^{2-5} ovate or semiovalate in cross section, lower canine caniniform; greatest skull length less than 48 mm; teats, 11, 13, 15, 17, or more; size, H&B, 114–185; T, 44–85; GSL, 23–43; habitat, Panama south through South American lowlands as far as Peru on the west, Uruguay and N Argentina on the east Monodelphinae
 Sole genus: *Monodelphis* Burnett, 1830
 (polytypic, figs. 8–10, 13)
 - 2. Karyotype $2n = 14$; tail longer than head and body combined, thinly hirsute, the scales fully exposed; paired superciliary spots conspicuous; manual claws weak, not extending beyond terminal phalanges; pectoral teats absent; ascending process of zygoma absent or rudimentary; crowns of i^{2-5} labiolingually compressed; lower canine more nearly incisiform than caniniform; greatest skull length more than 48 mm; teats, 9 (4–1–4); size, H&B, 190–310; T, 195–390; GSL, 49–68; habitat, from Nicaragua south into W Ecuador, and from Caribbean coast to Bolivia and N Argentina Metachirinae
 Sole genus: *Metachirus* Burmeister, 1854
 (monotypic, figs. 4, 9, 13)
- II. Tail prehensile, as long as or longer than combined head and body length; manual claws weak or stout, moderately to slightly or not protruding beyond terminal phalanges; throat gland present or absent; karyotype $2n = 14$, rarely 22; bullar floor with gap between petrous and alisphenoid components, the ectotympanic bone exposed; superior border of frontal bone rounded, square, beaded or ridged, with or without postorbital process; lambdoidal crest present or absent; sagittal crest absent; second or third premolar largest of series; articular facets of dorsal surface of calcaneus separate or continuous.
 - A. Tail seasonally incrassate (fat storing); 2 pairs pectoral teats present; throat gland present; manual

claws stout, protruding well beyond terminal phalanges; caudal scales annular; nasals more or less parallel-sided, not flared at frontomaxillary suture; weak lambdoidal crest present; third premolar larger than second; teats, 15 (7-1-7); paired articular facets of dorsal surface of calcaneus probably separate; size, H&B, 85-150; T, 90-160; GSL, 25-35; habitat, Peru, Bolivia, Chile, E Brazil, Paraguay, Uruguay, Argentina Thylamyinae

Sole genus: *Thylamys* Gray, 1843
(polytypic, figs. 8-10)

B. Tail never incrassate; pectoral teats present or absent; throat gland present or absent; manual claws weak, slightly or not protruding beyond tips of terminal phalanges; caudal scales spiral or annular; nasals expanded abruptly at frontomaxillary suture; lambdoidal crest present or absent; second premolar larger than fully erupted third, or subequal, rarely smaller; paired articular facets of dorsal surface of calcaneus continuous Marmosinae

Included genera: *Gracilinanus*, *Marmosops*, *Marmosa*, *Micoureus*

1. Pectoral teats absent; caudal scales spiral; superior border of frontal bone ridged, superior postorbital process usually pronounced or shelflike, the point sometimes reduced or absent; lambdoidal crest present; anteromedian process or strut of bullar portion of alisphenoid bone absent or rudimentary, not spanning foramen ovale.

(a) Karyotype $2n = 14$, throat gland absent; pelage thick, lax, crinkly; hypothenar and fourth interdigital pedal pads separate; brush of tail base long, thick, like back, extending 2 cm or more beyond rump; tail more or less uniformly colored, or blotchy, or with long terminal portion distinctly paler than proximal portion; superior border of frontal bone projected as ledge, superior postorbital process present; pm^2 larger to smaller than fully erupted pm^3 ; teats, 9, 11, 15; size, H&B, 130-200; T, 170-270; GSL, 35-50; habitat, tropical, subtropical parts of South America *Micoureus* Lesson, 1842
(figs. 5 (part), 8, 10)

(b) Karyotype $2n = 14$ or rarely 22; throat gland present in mature males; pelage short, adpressed; hypothenar and fourth interdigital pedal pads touching or coalesced; brush of tail base usually less than 2 cm long; tail more or less uniformly colored or with ventral surface slightly paler than dorsal, rarely blotchy or with terminal portion distinctly paler than proximal; superior border of frontal bone ridged, beaded, often with spine or point; pm^2 usually larger than fully erupted pm^3 , often subequal; teats, 9, 11, 13, 15, 19; size, H&B, 90-190; T, 125-230; GSL, 29-46; habitat, Mexico into Peru on the west, northern Argentina in the east *Marmosa* Gray, 1821
(figs. 5 (part), 8-10, 12)

2. Pectoral teats present or absent; caudal scales spiral or annular; superior border of frontal bone rounded, square, often beaded, sometimes with weak postorbital spine or point; lambdoidal crest present or absent; process or strut of anteromedian process of bullar portion of alisphenoid bone normally present and usually spanning foramen ovale.

(a) Pectoral teats absent; throat gland absent; middle pair of palmar pads fused; caudal scales spiral, the middle scutular hair thick, spiny, less than 2 scale rows long, lateral hairs fine; lambdoidal crest absent; buccal and lingual cingula of second and third premolars present or absent; teats, 9 (4-1-4); size excluding *Marmosops parvidens*, H&B, 95-160; T, 105-220; GSL, 26-42; *M. parvidens* alone, H&B, 90-115; T, 120-145; GSL, 25-32; habitat, tropical forests, Amazonia, Atlantic forest, Andean region of Venezuela, Colombia, Ecuador, Bolivia *Marmosops* Matschie, 1916
(figs. 5 (part), 8, 10)

(b) Pectoral teats present but not always clearly defined in dry skin; throat gland present but often hidden in fur; palmar pads separate or touching; caudal scales normally annular, 3 spiny hairs per scale, the middle more than 2 scales long; weak lambdoidal crest usually present; buccal and lingual cingula always present on third premolar; teats, 11, 13, 15; size, H&B, 70-135; T, 100-155; GSL, 22-32; habitat, tropical forests from Caribbean coast south into Brazil, Bolivia, Paraguay, and N Argentina *Gracilinanus* Gardner and Creighton, 1989
(infra p. 26)

Taxonomic History of Mouse Opossums, Subfamily Marmosinae

The taxonomy and nomenclature of mouse opossums was thoroughly reviewed by Tate (1933, p. 20) under the blanket generic name *Marmosa* Gray. The five species groups into which Tate divided the genus were subsequently reviewed by Creighton (1984), the characters of each restated and refined, the included species realigned. The revised arrangements led Gardner and Creighton (1989) to restructure the species groups of *Marmosa* into five genera, as follows (Tate's corresponding group names are in parentheses):

- Marmosa* Gray, 1821, genotype *Didelphis murina* Linnaeus (*murina* group)
- Micoureus* Lesson, 1842, genotype *Didelphis cinerea* Temminck (*cinerea* group)
- Thylamys* Gray, 1842, genotype *Didelphis elegans* Waterhouse (*elegans* group)
- Marmosops* Matschie, 1916, genotype *Didelphis incana* Lund (*noctivagus* group)
- Gracilinanus* Gardner and Creighton, 1989 (part, the *microtarsus* section of the *microtarsus* group); genotype, *Didelphys microtarsus* Wagner, 1842

The *Marmosa microtarsus* group was divided by Tate (1933, pp. 49, 185) into the *microtarsus* and *lepida* sections with the following taxa:

- microtarsus* section (= *Gracilinanus*)
 - emiliae* Thomas
 - microtarsus microtarsus* Wagner
 - microtarsus guahybae* Tate
 - agilis agilis* Burmeister
 - agilis beatrix* Thomas
 - agilis chacoensis* Tate
 - agilis buenavistae* Tate
 - agilis peruana* Tate
 - marica* Thomas
 - unduaviensis* Tate
 - aceramarcae* Tate
 - dryas* Thomas

Tate (1933, p. 203) regarded the *lepida* section as "artificial rather than natural." It included the following species (their generic positions, according to Creighton [1984] and Gardner and Creighton [1989], are in parentheses):

- lepida* section
 - lepida* (*Marmosa*)
 - juninensis* (*Marmosops*)
 - parvidens* (*Marmosops*)

The genus *Gracilinanus* is identical to Tate's *microtarsus* section, but with the subspecies he recognized included by Gardner and Creighton (1989) in the synonymies of their nominate species. *Marmosa unduaviensis* Tate was referred by Gardner and Creighton to *G. agilis* (*sensu stricto*) as were the later-described *blaseri* Miranda Ribeiro, 1936, and *rondoni* Miranda Ribeiro, 1936. *Marmosa agricola* Moojen, 1943, was identified with *Gracilinanus emiliae*.

The type data for all named forms of *Gracilinanus* are included in the relevant species accounts.

Genus *Gracilinanus* Gardner and Creighton— Gracile Mouse Opossums

Marmosa microtarsus group Tate, 1933, pp. 8, 10, 34, 43, 47, 49, 185—part, the *microtarsus* section only. Creighton, 1984, pp. 51, 98—characters; comparisons; species.

Thylamys Pine, 1977, p. 14—subgenus of *Marmosa*, part, the species of Tate's *microtarsus* section only. Reig, Kirsch, and Marshall, 1987, p. 7—part, the species of Tate's *microtarsus* section; part characters, distribution.

Gracilinanus Gardner and Creighton, 1989, p. 4.

TYPE SPECIES—*Didelphys microtarsus* Wagner, 1842, by original designation.

INCLUDED SPECIES—*aceramarcae* Tate, *agilis* Burmeister, *dryas* Thomas, *emiliae* Thomas, *kalinowskii* (new), *longicaudus* (new), *marica* Thomas, *microtarsus* Wagner, *perijae* (new).

ETYMOLOGY—From the Latin *gracilis* (gracile, slender) and Greek *nanos* (small, dwarf). Formation of the generic name by combining Latin and Greek words is valid but discountenanced.

Geographic Range

Gracile mouse opossums are widely distributed throughout the forested or wooded areas of South America from the Caribbean coast of Colombia and Venezuela on the north, to the Delta del Río Paraná in Buenos Aires, Argentina, on the south; from near sea level coast to coast to about 4500 m above into the temperate zone forests of the equatorial Andes, and to lower altitudes in higher southern Andean latitudes (fig. 1).

Gracilinanus has been recorded from all sylvan

biomes except those of Patagonia, the Guianas, and the Río Orinoco basins of Venezuela and Colombia excluding the Serranía de la Macarena of the Cordillera Oriental. The genus is unknown from the Amazonian basin except in its southern and western peripheries and shores of the middle and lower parts of the main stream itself. It has been recorded from the vast cerrado of central Brazil but actual capture was from gallery forest or patches of dry upland forest. The genus has not been recorded from the Río Magdalena valley of Colombia but is known from the lower Río Atrato basin in the extreme northwest. It is unknown in Central America and the West Indies. Most of the distributional gaps within the known boundaries of the geographic range contain accessible and apparently suitable habitats for *Gracilinanus*.

Sympatry

The wide distribution of *Gracilinanus* encompasses some part of the range of all other genera of marmosid opossums except that of the Patagonian *Lestodelphys*. Sympatry, as understood here, however, is between congeneric species. Those of the genus *Gracilinanus* are between *G. dryas* and *G. marica* in parts of the Cordillera Oriental of northern Colombia and northwestern Venezuela; some populations of *G. agilis* may be sympatric with *G. emiliae* in northeastern Brazil; others of *G. agilis* may occur together with *G. kalinowskii* in the Chanchamayo area of the Peruvian Andes. Whether or not sympatric species of gracile opossums share the same ecological niches is unknown.

Habitat and Habits

NESTING—Murine opossums dwell in trees or shrubs. That gracile opossums may actually construct nests has not been reported. Attached and unattached suckling young stay with the pouchless mother wherever she goes. The weaned probably shift for themselves and shelter opportunistically.

FORAGE—Many if not most species forage on the ground. They are particularly attracted to above- or on-ground traps baited with ripe fruit, peanut butter, or flesh. Negative trapping results in some parts of the range, however, suggest that certain arboreal species of murine opossums rarely

if ever descend to the ground in periodically inundated areas, even during the dry season. Food, particularly insects, and water are always available aboveground. Species of *Gracilinanus* known from one or two specimens only may be strictly canopy dwellers with descent to the forest floor accidental, forced, or particularly enticed. Common, widespread species such as *Gracilinanus agilis* are regular ground-level foragers and may even nest amid forbs.

DIET—Gracile opossums are insectivorous, carnivorous, and frugivorous. Their teeth are not adapted for gnawing, grinding, or scraping, their jaws too weak for cracking anything harder than a beetle's carapace. These tiny opossums relish sweet pulpy food and plant exudates and evidently have a predilection for the ripe banana and peanut butter baits that lure them into traps. They cannot bite through bark or the hard rind of ripe fruit but do feed on the pulp or exudate exposed by other predators.

Function of the projecting, cylindrical, but non-occluding first upper incisors can only be surmised. They may be used as prongs for extracting grubs, worms, or other morsels and/or for grooming, but they seem too weak for any of these functions.

ENEMIES AND DEFENSE—Two individuals of *G. agilis* I captured in an arboreal live trap reacted to confrontation with the stereotypical opossum response. Each animal reared up on its hind legs, forearms outstretched, palms turned outward, mouth open wide and hissing. It is unlikely that this behavior would intimidate a predator. If prodded with a stick, the mouse opossum will, if it can, seize it with its teeth and hang on. Feigning death, a common opossum ploy, has not been recorded for mouse opossums. Most frequent enemies are owls, snakes, lizards, or any carnivore large enough to gulp down a mouse-size morsel.

LOCOMOTION—Movements aboveground are like those of other arboreal opossums with long prehensile, nonincrassate tail. The short swift quadrupedal gaits are interchanged with overhand climbing up or down. The opposable fingers and toes grip tail or vine firmly (fig. 3). Volar pads also serve for gripping and clutching. The front claws are weak, but the longer, heavier hind claws can grapple the bark in headfirst descent. The tail, used for support and balance, also serves in lieu of a hanging vine. By embracing a slender overhead branch with the tip, the suspended animal has been seen to climb up and swing down by its tail.

TAIL FUNCTION IN SEXUAL BEHAVIOR—Barnes

(1968, p. 255, fig. 2) observed that males in the wire cages of a laboratory colony of *Marmosa robinsoni* hang by the tail during copulation. It was further noted by Barnes and Barthold (1969, p. 479) that "erection of the male's penis does not occur until he has obtained purchase with the tail, and close observation reveals that a tension must be developed in the tail if erection and insertion are to be completed. Pairs placed in solid-walled cages may achieve the mounted position but insertion does not take place." I have found no more reference to similar behavior in these and other animals. The description may be of a specialized use of the long prehensile tail of marmosines or, perhaps, an isolated case.

BREEDING—Tate (1933) found Bolivian *Gracilinanus agilis* breeding or nursing in April and December. These widely separated months suggest year-round reproductive activity or two breeding seasons. Mares et al. (1989) trapped *G. agilis* of all ages and breeding conditions throughout the year in gallery forests of the central Brazilian cerrado. When food is abundant, breeding may be continuous.

SOCIAL RELATIONS—Like all other didelphoids, gracile opossums are solitary. Opossums of any species may congregate at a feeding place but only for feeding. Social relationships are limited to short sexual encounters between conspecifics.

TORPIDITY—Of the 14 males and 2 females live-trapped repeatedly in a cerrado study area in Brasília, D.F., by Nitikman and Mares (1987, p. 85), 9 never made use of cotton balls provided in all their traps for insulation. "During the cool winter mornings, this species often was found torpid in the traps. Torpidity was apparently an effective response against low temperatures; despite the lack of an insulating nest, *M. agilis* had the lowest rate of trap mortality." Other small mammals trapped were *Monodelphis americana* and eight recorded species of sigmodontine rodents.

Diagnostic Characters of Genus *Gracilinanus*

Size comparatively small, H&B, between 70 and 135 mm, T, 100–155 mm, GSL, 22–32 mm; prime teat formulas, 5–1–5 = 11, 6–1–6 = 13, 7–1–7 = 15 including 2–0–2 pectoral; caudal scales small, arrangement usually annular, sometimes spiral at least on basal one-half (fig. 2); palmar and plantar surfaces little or not granular, pads separate (fig.

3); skull (figs. 6–11) with muzzle attenuate, nasal tips pointed; superior borders of frontals square, rounded, or beaded, parallel-sided in some, divergent in others, often with a midfrontal constriction, or a blunt angle or spine; nasal bones moderately flared at frontomaxillary suture; braincase smooth or with weak temporal ridges; lambdoidal crest poorly defined except in old individuals; palate (fig. 9) usually well fenestrated, the mesolateral fenestrae usually present, postero-medial fenestrae sometimes absent or poorly defined (*G. kalinowskii*); tympanic bulla (figs. 10, 11) tripartite with inflated wing of alisphenoid and pars petiotica widely separated, ventrally exposed ectotympanic bone suspended between the two bones partially concealed by alisphenoid; antero-medial process or strut spanning foramen ovale nearly always present; molars (figs. 6–9) dilambdomorphic, tritubercular; i^1 about same size as i^4 or slightly larger; pm^2 usually larger than fully erupted i^3 ; inner and outer cingula of upper premolars complete.

REMARKS—The genus as originally defined by Gardner and Creighton (1989) is based on the *Gracilinanus agilis* group (p. 31 below) composed of the six larger species recognized at the time. The small *G. kalinowskii* (new) is aberrant and would not be included in the genus as originally defined. The same probably applies to *Gracilinanus* sp. (p. 42 below), a large species. A definitive description of the genus awaits more nearly complete knowledge of its components. Targeted field collecting and study of other museum collections may result in better than doubling the nine presently recognized number of species.

Variation and Comparisons

Coloration

Hair color is determined by either or both of two pigments or melanins. Eumelanin, the phylogenetic oldest, is dark brown or "blackish" but may be diluted to pale brown, drab, or gray to nearly white. The second pigment, pheomelanin, is bright orange or "reddish" and may be diluted to ochraceous or yellowish, pale buff or cream, to nearly white. Hair without pigment is colorless or translucent but may appear white. The pigment granules are formed by the melanocytes in the hair follicles and deposited into the medulla of the hair. A banded or agouti pattern is produced by a pro-

cess of switching from deposition of eumelanin to pheomelanin in the continuously growing hair. The resultant agouti pattern of alternating color bands, usually of the terminal half of the hair, is the primitive form from which all other color patterns can be derived. Color of the basal or hidden portion of the hair is typically a tone of eumelanin. Of the three principal types of hair, each distinguished by length and texture, the banded or agouti is generally confined to the soft, straight midlength cover hairs. The longer, stiff, projecting guard or sensory hairs are usually entirely blackish. Fine, short, often crinkly woolly hairs or underfur, thin or absent in marmosine opossums, are usually eumelanin pigmented. For more detailed accounts of mammalian tegumentary coloration, see Hershkovitz (1968, 1970, 1977).

The agouti is the dominant and presumably the most concealing pilary color pattern among small nocturnal prey mammals such as marmosine opossums. In these, the agouti pattern may extend over most or all upper parts and sides of the body. Pelage of underparts, not generally exposed to view, is usually bicolor, the hair bases eumelanin, the terminal portion pheomelanin, or the hair may be monochrome, the color a tone of either pigment, usually pheomelanin, or unpigmented white.

In *Gracilinanus*, dorsal coloration of cover hairs is a modified agouti or tricolor pattern, with hair base eumelanin (dark brown to drab or grayish), terminal portion broadly banded pheomelanin (orange to buffy), extreme tips eumelanin or blackish. Hairs of underparts are bicolor with base eumelanin, terminal portion tones of pheomelanin ranging from orange through yellow or cream, to white or colorless. Pelage of glandular areas may be more intensely pigmented pheomelanin than that of surrounding parts. A facial pattern marked by blackish eye ring, and a pale (pheomelanin) upper surface of muzzle, is common to nearly all marmosid opossums including all species of *Gracilinanus*. Ears are brown, scrotum unpigmented in *Gracilinanus*, *Marmosops*, and *Metachirus*; unpigmented to pigmented in *Marmosa* and *Micoureus*, apparently according to species; pigmented in *Thylamys* and *Monodelphis*.

Among the species of *Gracilinanus*, *G. dryas* is most saturate eumelaninistic on both upper parts and underparts; *G. microtarsus* is most saturate pheomelaninistic. *G. kalinowskii* (two specimens) and *G. longicaudus* (holotype) are the only known species of the genus with underparts entirely whitish.

The blackish eye ring (see frontispiece) is narrow

in most species of *Gracilinanus*, broader than average in *G. microtarsus*, similarly broad in *G. dryas* but with a band extending from outer canthus of eye along side of muzzle to tip of rhinarium as in *G. perijae*, and perhaps in some individuals of *G. agilis*; in *G. kalinowskii*, the band extends from inner canthus of eye to ear base; ears pigmented dark brown terminally, paler basally, often bright yellowish.

Skin of tail is brownish; the hairs are three per scale with the central one longest and thickest. Caudal hairs of dorsal surface are brownish, the lateral ones paler than the central, or white. Ventral hairs may be similar, or paler, or entirely whitish, and as long as or longer than the dorsal hairs. Variation in caudal pilary coloration and length may be greater among individuals than among species.

Color and Environment

Tate (1933, p. 7) surmised that the coloration and environments of murine opossums are correlated. Opossums of dry regions were conceived as dominantly grayish or pale, and those of humid regions as dark or warmly colored, as is often the case in small terrestrial rodents. Inconsistencies between the correlations noted by Tate, and many more evident in his descriptions of individuals, fairly annul the hypothesis. Nearly all marmosine opossums are mainly or almost entirely arboreal; none roams the panoramic landscapes vaguely described as habitats or environments by Tate. Furthermore, all habitats are subject to daily and seasonal changes in temperature and atmospheric humidity. Perhaps Tate intended to suggest that opossum coloration may be concealing within its particular niche. In the world of nocturnal carnivorous arboreal opossums, however, sound, movement, body odor, and body heat are much more revealing than external coloration is concealing, if indeed it does conceal at night. In any event, color vision of nocturnal nonhuman predators has yet to be evaluated in terms of successful predation on marmosine opossums.

Caudal Scale Arrangement (fig. 2)

As a rule, the arrangement of caudal scales is annular in *Gracilinanus*, a character shared with *Thylamys* and *Metachirus*. In *G. kalinowskii*, however, the arrangement of scales appears spiral in

the holotype but annular in the paratype. A spiral arrangement also occurs in the tail of a dark immature individual (FMNH 23945) from Cocos, Maranhão. The pattern appears to be spiral on the proximal part of the tail of one individual and annular in another (FMNH 70981) of two samples of *G. dryas* from Bogotá. The same condition is evident in the tails of a few *Metachirus*. The arrangement is spiral in specimens examined of *Marmosops*, *Micoureus*, *Marmosa murina*, and *M. robinsoni*.

Ungues (fig. 3)

New World marsupials are provided with claws on all digits except the hallux, which lacks an unguis, and the pollex, which in the Caenolestidae bears a well-formed rounded nail-like callous, not a claw.

The marmosine ungues are fairly uniform in size and shape. Those of the manus are short, thin, and adpressed and do not surpass the tips of the digits in *Gracilinanus*, *Marmosops*, and *Marmosa*. They are longer and stouter in *Micoureus*. Pedal claws are more or less recurved and stout and extend well beyond the digital tips in *Marmosops* and *Micoureus*; they are weaker and shorter in *Marmosa* and *Gracilinanus*; and those of *G. kalinowskii* are the longest and stoutest.

Among other Marmosidae, manual and pedal claws of *Monodelphis* are longest and sharpest, extending well beyond the digits. Those of *Lestodelphys* are nearly as long but more prominent because of the short stubby digits. Claws of *Metachirus* are weak and short, differing little from those of the Marmosinae.

Claws of the Didelphidae are stout and recurved and extend beyond the digital tips of hands and feet. The manual claws of *Chironectes*, however, are short, needlelike, and apparently functionless.

The Dromiciops (Microbiotheriidae) ungues are weak and without extension to the digital tips. Those of the pes are stronger and slightly recurved and extend to or slightly beyond the digital tips.

Mammae (table 1)

Mammae or teats are arranged bilaterally with one or rarely a few medially in the abdominal region, the total number usually odd. In most marmosids, the lateral teats are inguinal and abdominal and also pectoral in some. The *prime* formula

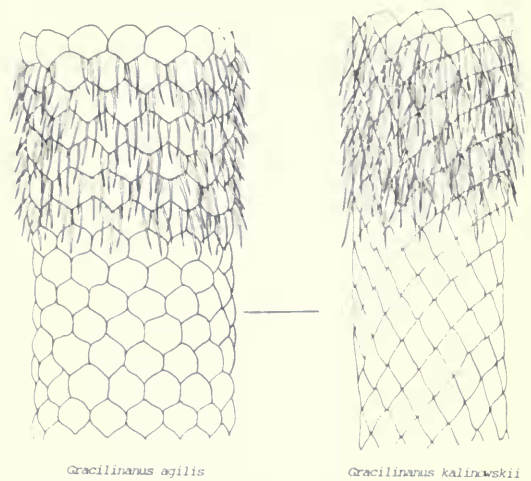


FIG. 2. Caudal hair extends length of tail, but shown partially to reveal scale patterns. Scutulation spiral in *G. kalinowskii*; annular in *G. agilis*. Bar = 1 mm.

for *Gracilinanus* is $7-1-7 = 15$, of which the pectoral is $2-0-2 = 4$, the abdominal-inguinal, $5-1-5 = 11$. The *functional* teat formula may be the same or less, depending on the number of attached young. Unused nipples are more or less resorbed. Pectoral mammae, anteriormost retentions of the once continuous pair of milk lines, are also present in *Thylamys*, *Monodelphis*, and, according to Tate (1933, p. 36), "probably in *Lestodelphys*."

The abdominal-inguinal mammary field is not contrastingly pigmented in *Gracilinanus*. A distinctively colored field, however, is present in nursing females of *Marmosa*, *Micoureus*, *Marmosops*, and *Metachirus*. The field is pigmented in the fully pouched Didelphidae and partially pouched Caluromyidae.

Gular Glands

Gular glands are usually present in *Gracilinanus*, *Marmosa*, *Thylamys*, *Lestodelphys*, *Monodelphis*, and *Metachirus* and absent in *Micoureus* and *Marmosops*. The glandular area may be marked by a patch of deeply pigmented hair or by an ovate bare spot. Neither marker is present in the two females of *G. kalinowskii*.

Cloaca

In *Gracilinanus*, urogenital and rectal tracts open into a common chamber, the cloaca. The same

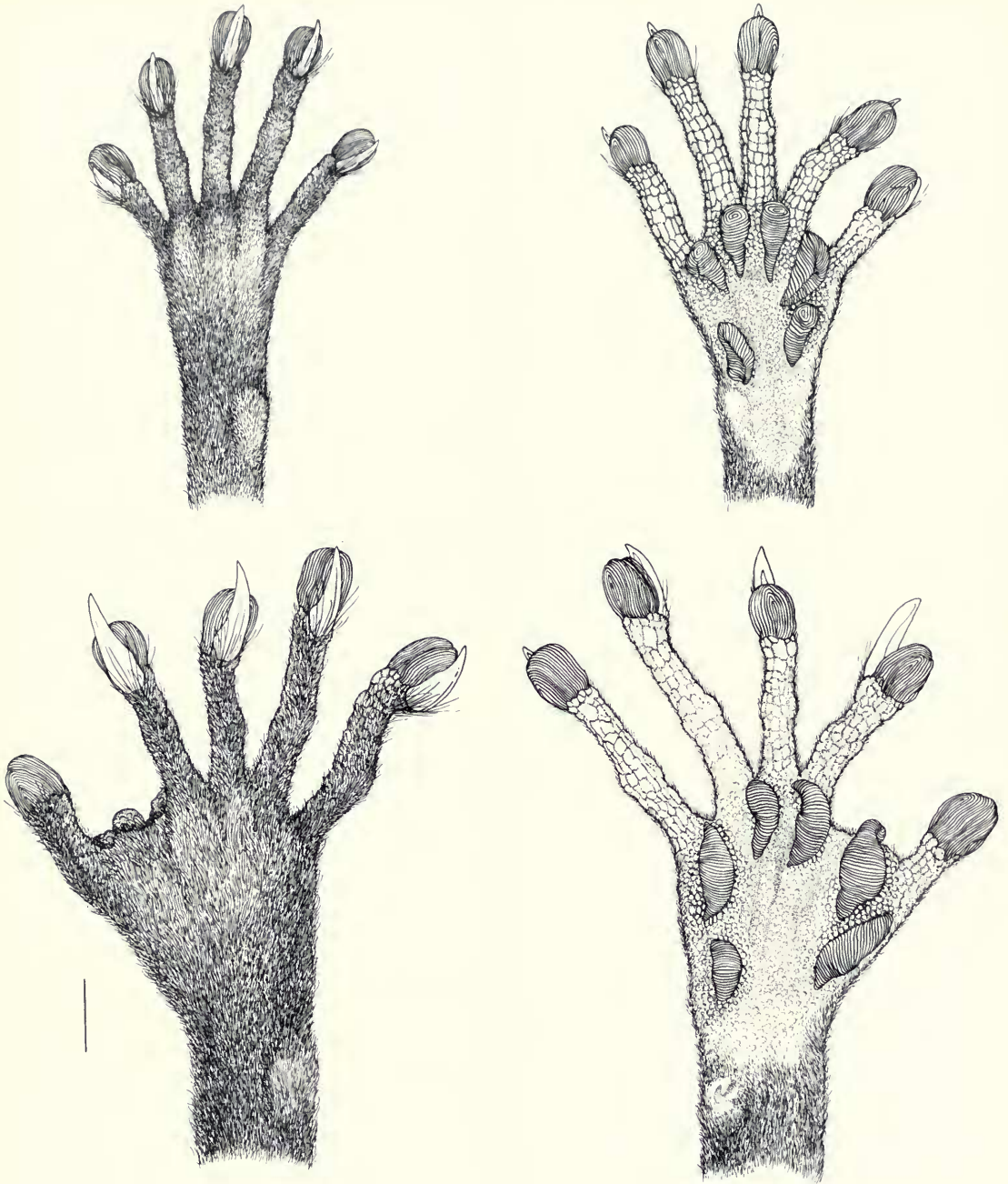
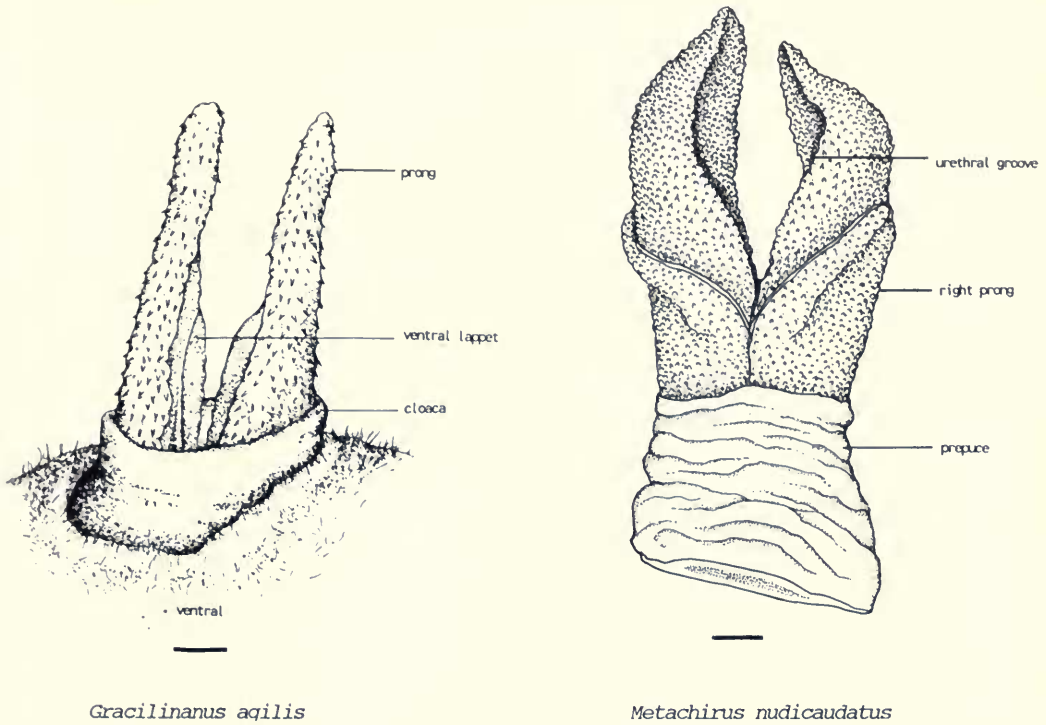


FIG. 3. *Gracilinanus microtarsus* cheiridia (FMNH 136829). Dorsal and ventral surfaces of right hand (upper) and foot (lower). From spirit-preserved specimen. Bar = 1 mm.

system occurs in some species of *Marmosa*, *Caluromyidae* except *Caluromysiops*, *Caenolestidae*, and *Microbiotheriidae*. The male urogenital opening in the marmosid genera *Marmosops*, *Micoureus*, and *Metachirus* is separated in the cloaca

from the rectal outlet by the perineal membrane continuous with the pubic integument. This semi-cloacal or cloacal-perineal system, restricted to males, represents a developmental grade between unmodified cloaca to complete perineal separation



Gracilinanus agilis

Metachirus nudicaudatus

FIG. 4. Glans penis of *Gracilinanus agilis* (ventral aspect; bar = .05 mm) and *Metachirus nudicaudatus* (dorsal aspect; bar = 3 mm).

between urogenital and rectal ducts in both sexes with cloacal elimination. The perineal or non-cloacal is the prevailing system in the Didelphidae, some Australian Macropodidae, Phalangeridae, and all eutherians except *Ochotona* (Lagomorpha), and most if not all species of Insectivora.

The cloaca is precaudal in all marsupials and eutherians, but in the microbiotheriid *Dromiciops* it is basicaudal or postpelvic as in monotremes and reptiles (Hershkovitz, 1992).

Glans Penis (figs. 4, 5)

The glans penis of fully mature *Gracilinanus agilis* is bifid. That of examined suckling young is simple or single-headed. As the penis develops, a division appears along the middle of the urethral canal. Each half of the channel remains as a groove or trough on the medial side of each prong or horn of the bifurcated glans penis. The design of the bifid glans penis suggests that when opposite parts are in contact, the restored urogenital duct serves for urination only. In copulation, erection separates the prongs, switches off the urinary system,

and switches on the ejaculatory. A morphological correlation between the bifid glans penis and double vagina is not apparent.

Among remaining Marmosidae, the glans penis is bifid in the mature and simple in the immature of all examined of *Marmosops*, *Micoureus*, *Thylamys*, and *Metachirus*. In *Marmosa* (*M. mexicana*), the glans remains undivided but may be divided in other species currently assigned to that genus.

The bifid glans also occurs among specimens examined of *Caluromys*, *Didelphis*, *Philander*, and *Caenolestes*. It is simple in *Caluromysiops*, *Chironectes*, and perhaps *Dromiciops*. In nearly all samples, the outer surface of the glans penis is invested with miniature spines distinctive for each species. In most if not all glandes, the outer surface is also marked by fine spiral grooves or canals and by lappets or other fleshy extrusions, which may be erectile. Marsupials lack baculum.

The undivided glans penis of some adult and all immature marsupials examined is the primitive state retained as noted in some metatherians and in all living eutherians. It appears to be homologous with the penis (and clitoris) of turtles and

TABLE 1. Teat formulae of Marmosidae.*

Taxon	Prime teat formulae [functional formulae in brackets]	Source
Marmosidae		
Marmosinae		
<i>Gracilinanus</i> (formulae include pectoral mammae 2-0-2)		
<i>agilis</i>	[6-1-6 = 13]	Tate, 1933, p. 196, fig. p. 35
<i>microtarsus</i>	7-1-7 = 15	Tate, 1933, pp. 186, 193
<i>marica</i>	5-1-5 = 11	Herskovitz, field notes (FMNH)
<i>Marmosops</i>		
<i>carri</i>	4-1-4 = 9	Tate, 1933, fig. p. 35
<i>impavidus</i>	4-1-4 = 9 (3, includes holotype of <i>handleyi</i>)	Herskovitz, field notes (FMNH)
<i>impavidus</i>	4-1-4 = 9	Tate, 1933, p. 184
<i>impavidus</i>	[3-1-3 = 7]	Tate, 1933, fig. p. 35
<i>impavidus</i>	[2-1-2 = 5]	Tate, 1933, p. 185
<i>incanus</i>	[3-1-3 = 7]	Tate, 1933, p. 166
<i>noctivagus</i>	4-1-4 = 9 (3)	Herskovitz, field notes (FMNH)
<i>parvidens</i>	4-1-4 = 9	Herskovitz, field notes (FMNH)
<i>parvidens</i>	[3-1-3 = 7]	Pine, 1981, p. 66
<i>Marmosa</i>		
<i>canescens</i>	[4-1-4 = 9]	Tate, 1933, p. 141
<i>canescens</i>	[4-1-4 = 9]	Tate, 1933, p. 143
<i>casta</i>	7-1-7 = 15	Tate, 1933, p. 117
<i>chapmani</i>	7-1-7 = 15 (2)	Thomas, 1888, p. 345 (as " <i>murina</i> ")
<i>chapmani</i>	7-1-7 = 15	Tate, 1933, fig. p. 35
<i>chapmani</i>	[5-1-5 = 11]	Tate, 1933, p. 112
<i>lepida</i>	[3-1-3 = 7]	Tate, 1933, fig. p. 206
<i>mexicana</i>	7-1-7 = 15	Tate, 1933, fig. pp. 35, 128
<i>mexicana</i>	[6-1-6 = 13]	Gewalt, 1968, p. 288
<i>murina</i>	[13]	Eisentraut, 1970, p. 159 (as " <i>murina</i> ")
<i>murina</i>	5-1-5 = 11 (3)	Carlsson, 1903, p. 491
<i>murina</i>	5-1-5 = 11	Herskovitz, field notes (FMNH)
<i>murina</i>	5-1-5 = 11	Tate, 1933, p. 89
<i>murina</i>	5-1-5 = 11	Thomas, 1888, p. 345, note
<i>murina</i>	5-1-5 = 11	Herskovitz, field notes (FMNH)
<i>murina</i>	5-1-5 = 11	Herskovitz, field notes (FMNH)
<i>murina</i>	5-1-5 = 11	Herskovitz, field notes (FMNH)
<i>murina</i>	[9]	Herskovitz, field notes (FMNH)
<i>quichua</i>	5-1-5 = 11	FMNH, 19352 (topotype)
<i>robinsoni</i>	7-1-6[=7] = 15	Tate, 1933, p. 111 (as " <i>mitis</i> ")
<i>robinsoni</i>	6-1-6 = 13	Enders, 1935, p. 408 (as " <i>isthmica</i> ")
<i>robinsoni</i>	6-1-6 = 13	Thomas, 1888, p. 345, note (as " <i>murina</i> ")
<i>robinsoni</i>	9-1-9 = 19	Tate, 1933, pp. 111, 119
<i>robinsoni</i>	[6-1-6 = 13]	Herskovitz, field notes (FMNH)
<i>robinsoni</i>	[6-1-6 = 13] (20)	Godfrey, 1975, p. 553
<i>robinsoni</i>	[4-1-4 = 9] (3)	Herskovitz, field notes (FMNH)
<i>robinsoni</i>	[5-1-5 = 11]	Herskovitz, field notes (FMNH)
<i>robinsoni</i>	7-2-7 = 16 (2)	Herskovitz, field notes (USNM)
<i>robinsoni</i>	7-1-7 = 15	Herskovitz, field notes (USNM)
<i>robinsoni</i>	4-1-4 = 9	Herskovitz, field notes (USNM)
<i>robinsoni</i>	17	Herskovitz, field notes (USNM)
<i>robinsoni</i>	7-1-7 = 15	FMNH
<i>rubra</i>	4-1-4 = 9	Herskovitz, field notes (FMNH)
<i>rubra</i>	[3-1-3 = 7]	Herskovitz, field notes (FMNH)
<i>Micoureus</i>		
<i>cinereus</i>	[5-5-5 = 15]	Tate, 1933, fig. p. 35 (as " <i>constantiae</i> ")
<i>cinereus</i>	[6-1-7 = 14]	Tate, 1933, fig. p. 35 (as " <i>alstoni</i> ")
<i>cinereus</i>	7-1-7 = 15	Tate, 1933, pp. 71-74 (as " <i>constantiae</i> ")
<i>cinereus</i>	4-1-4 = 9	FMNH

TABLE 1. *Continued.*

Taxon	Prime teat formulae [functional formulae in brackets]	Source
<i>demerarae</i>	5-1-5 = 11	Tate, 1933, p. 60
<i>demerarae</i>	[4-1-4 = 9]	Tate, 1933, fig. p. 35 (as " <i>alstoni</i> ")
<i>demerarae</i>	5-1-5 = 11	Tate, 1933, p. 69 (as " <i>alstoni</i> ")
<i>demerarae</i>	5-1-5 = 11	Tate, 1933, pp. 71, 73 (as " <i>domina</i> ")
<i>germanus</i>	4-1-4 = 9	Tate, 1933, pp. 71, 80
<i>germanus</i>	4-1-4 = 9 (2)	Hershkovitz, field notes (FMNH)
<i>phaeus</i>	4-1-4 = 9	Hershkovitz, field notes (FMNH)
Thylamyinae		
<i>Thylamys</i> (formulae include pectoral mammae 2-0-2)		
<i>elegans</i>	7-1-7 = 15	Tate, 1933, fig. pp. 35, 210, 213, 215
<i>elegans</i>	7-1-7 = 15	Mann, 1978, fig. p. 17
<i>elegans</i>	7-1-7 = 15	Tate, 1933, fig. pp. 35, 221 (as " <i>janetta</i> ")
<i>elegans</i>	7-1-7 = 15	FMNH (pectoral mammae not detected)
<i>pusillus</i>	7-1-7 = 15	Thomas, 1888, p. 342
<i>pusillus</i>	[6-1-6 = 13]	Carlsson, 1903, p. 491
Lestodelphinae		
<i>Lestodelphis</i>		
<i>halli</i>	(inguinal, abdominal, pectoral = ?)	
Monodelphinae		
<i>Monodelphis</i>		
<i>americana</i>	5-5-5 = 15	Thomas, 1888, p. 363
<i>brevicaudata</i>	5-1-5 = 11	Thomas, 1888, p. 357
<i>domestica</i>	5-3-5 = 13 (4)	Thomas, 1888, p. 359
<i>henseli</i>	11-5-11 = 27	Thomas, 1888, p. 17
<i>sorex</i>	5-3-5 = 13	Carlsson, 1903, p. 492
Metachirinae		
<i>Metachirus</i>		
<i>nudicaudatus</i>	5 to 9	Osgood, 1921, p. 75
<i>nudicaudatus</i>	4-1-4 = 9	Thomas, 1888, p. 335
<i>nudicaudatus</i>	4-1-4 = 9 (3)	Hershkovitz, field notes (USNM)
<i>nudicaudatus</i>	9	Enders, 1935, p. 412
<i>nudicaudatus</i>	[4-1-3 = 8]	Hershkovitz, field notes (FMNH)

* When sample number is more than 1, number is in parentheses. Identifications are from sources cited; formulae from Hershkovitz field notes are of freshly killed animals, the specimens in FMNH or USNM; spirit-preserved specimens in the museum collection are shown as FMNH. Species are arranged alphabetically.

crocodiles (Owen, 1866, p. 582). The hemipenis of snakes and lizards is functionally analogous but not homologous.

Although material at hand is too poor for fuller analysis, it is obvious that male external genitalia of marsupials, no less than those of eutherians, are important taxonomic tools for distinguishing species and defining genera. A few samples are illustrated in figures 4 and 5.

Frontal Bone (figs. 6-8)

In *Gracilinanus*, superior borders may be rounded, square, or raised as weak temporal ridges

that disappear at or on the parietal bones. The borders behind the postorbital constriction may be parallel or slightly divergent in all species but are most widely spread in *G. kalinowskii*, in which the width between measured at frontoparietal suture is about twice that of postorbital constriction. In adults of other congeners, the spread is usually less than 1.5 times the constriction. The same limitation applies to young with relatively wider braincases than in adults.

Incipient postorbital processes are present in most skulls examined of *G. agilis* but in no other species of *Gracilinanus*.

Postorbital processes are well developed in *Marmosa* and *Micoureus*, weak or merely indicated in

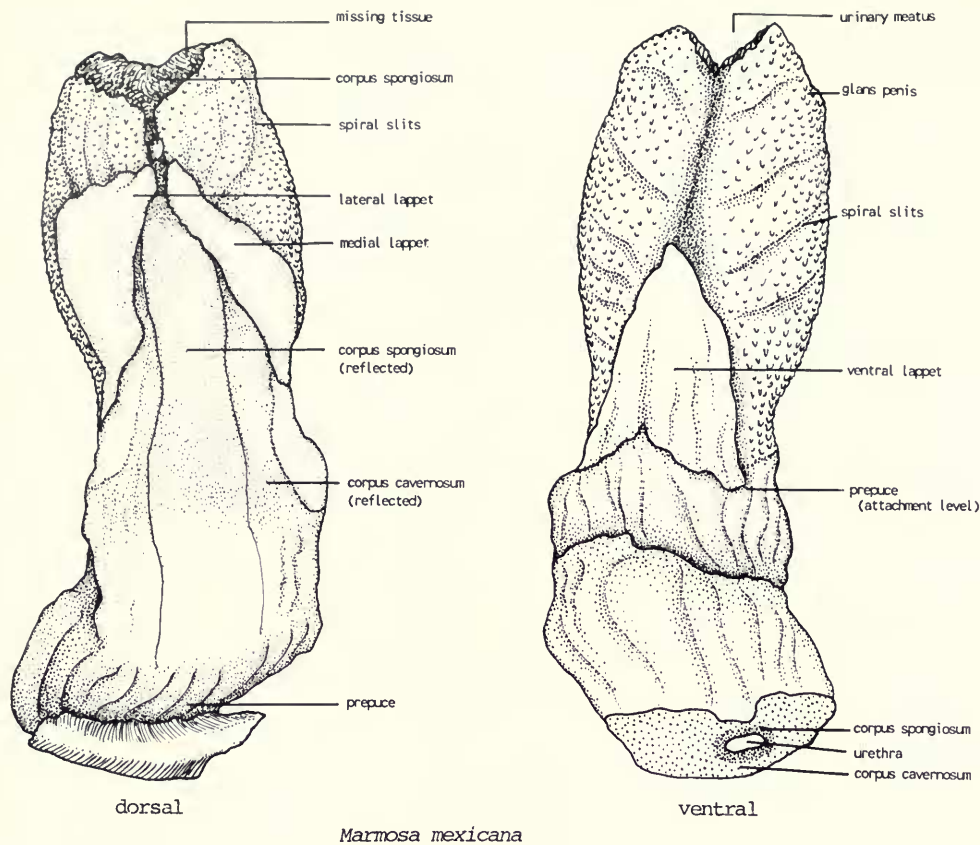


FIG. 5 (part). Glans penis of *Marmosa mexicana* (bar = 3 mm).

Lestodelphys and *Marmosops*, and absent in *Thylamys*, *Monodelphis*, and *Metachirus* (fig. 8). They are well developed in all Didelphidae and Caluromyidae.

Sagittal Crest (fig. 8)

The temporal ridges do not unite to form a sagittal crest in *Gracilinanus*, *Marmosops*, *Marmosa*, *Micoureus*, *Thylamys*, or *Metachirus*. A low, weak crest is present in *Monodelphis* and *Lestodelphys*. It is absent in *Glironia*, well developed in all Didelphidae (*Didelphis*, *Philander*, *Chironectes*, *Lutreolina*), present in the caluromyids *Caluromys lanatus* and *C. philander*, in males and old females of *C. derbianus*, and in *Caluromysiops*.

Nasal Bones (figs. 6-8)

The nasal bones of *Gracilinanus*, like those of nearly all didelphoids, are narrow, fairly parallel-sided for their anterior two-thirds, then abruptly flared to the nasomaxillary suture and as abruptly contracted terminally to the frontal sutures. Nasals of caenolestids and *Dromiciops* (Microbiotheriidae) are similar. Those of *Thylamys*, the lone exception among living American marsupials, are virtually parallel-sided sometimes with slight expansion posteriorly. Nasal bones among Australian marsupials vary from parallel-sided to expanded posteriorly with or without flare according to species. Parallel-sided nasal bones appear to be the basic form from which all others may have been derived.

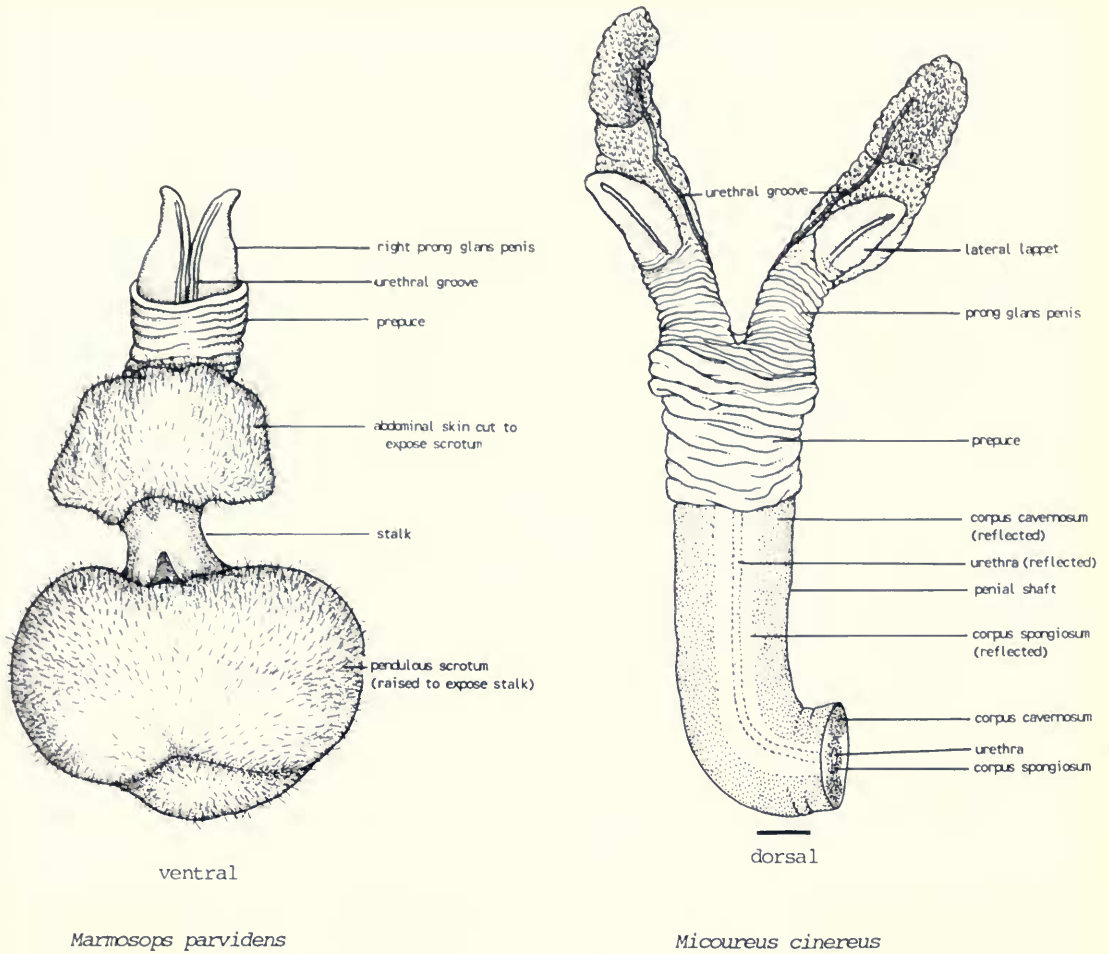


FIG. 5 (part). Glans penis of *Marmosops parvidens* and *Micoureus cinereus* (bar = 3 mm).

Palatal Vacuities (fig. 9)

Ossification of the primordial mesenchymatous palate in the ancestral therian may not have advanced much beyond the inner alveolar border of each tooth row. That of the didelphoid palate is usually incompletely ossified. In some species, the ossified portions may be thin or translucent in whole or part. Ossifications apparently proceed from all sides of each palatal lamina. Paired vacuities in the adult palatal bones result where ossification of opposite segments of each lamina is incomplete. Palatal perforations in *Gracilinanus* and other marsupials are the following:

1. Premaxillary or incisive foramina, not true vacuities. Nearly or entirely defined by borders

of the premaxillary bone. Foramina remain open in all mammals.

2. Maxillopalatine, or mesolateral, vacuities. Elongate openings of anterior portion of maxillary and posterior portion of palatine bones; persistent in most didelphoids but with posterior or palatine portion sealed first by bone.
3. Posteromedial or palatine vacuities. Irregularly rounded with one on each side of suture between palatine bones; they are discrete in *Gracilinanus*, usually confluent with the maxillary-palatine vacuities in *Dromiciops* and caenolestids, and greatly reduced or closed by ossification in most didelphids.
4. Maxillary or lateral vacuities. Present on medial side of each maxillary tooth row; the first to disappear in all didelphids.

GRACILINANUS



FIG. 6. *Gracilinanus* skulls, dorsal and ventral aspects: *G. kalinowskii* (FMNH 89991, ♀, holotype); *G. longicaudus* (FMNH 87924, ♂, holotype); *G. perijae* (USNM 280881, ♂, holotype); *G. marica* (FMNH 54645, ♂, topotype). White bar = 1 cm; see figures 9 and 11 and table 5 for actual measurements.

5. Posterolateral vacuities or foramina. Defined by short process of posterolateral border of maxillary bone and connecting posterolateral process of palatine bone. As foramina they persist unossified but their size may be extremely reduced in some didelphoids, in rare cases closed among caluromyids.

Each vacuity varies in size and, with the exception of the foramina, may be continuous with a neighboring vacuity in an early developmental stage. Nevertheless, the type and order of persistence of vacuities appear to be more or less fixed in most species. With allowance for normal variation, the pattern in each taxon is a stage or frame in the ossification process.

The palates of *Lestodelphys*, *Thylamys*, and most species of *Marmosa* are nearly as perforate as that

of *Gracilinanus*, but with the maxillary or mesolateral pair of vacuities vestigial or ossified. Least perforate palates among pouchless opossums are those of *Metachirus* and *Monodelphis*.

The bony palate of the Caluromyidae is nearly entirely ossified, and that of *Caluromysiops* (fig. 9) virtually entire. A pair of minute midpalatal and sometimes pinpoint-sized posterolateral vacuities persist in *Caluromys*. The midpalatal and posterolateral vacuities persist in *Glironia* (fig. 9).

Palates of the didelphids *Philander*, *Didelphis*, *Chironectes*, and *Lutreolina* are marked by large maxillary-palatine vacuities. The rounded posteromedial vacuities are fairly large in *Didelphis*, and small or absent in the others.

The palate of *Dromiciops* (fig. 9) is about half ossified, and that of caenolestids (fig. 9) about as little or less.



FIG. 7. *Gracilinanus* skulls, left side of same shown in figure 6, with lateral aspect of corresponding mandibles (that of *G. kalinowskii* is the right). White bar = 1 cm; see figure 9 and table 5 for actual measurements.

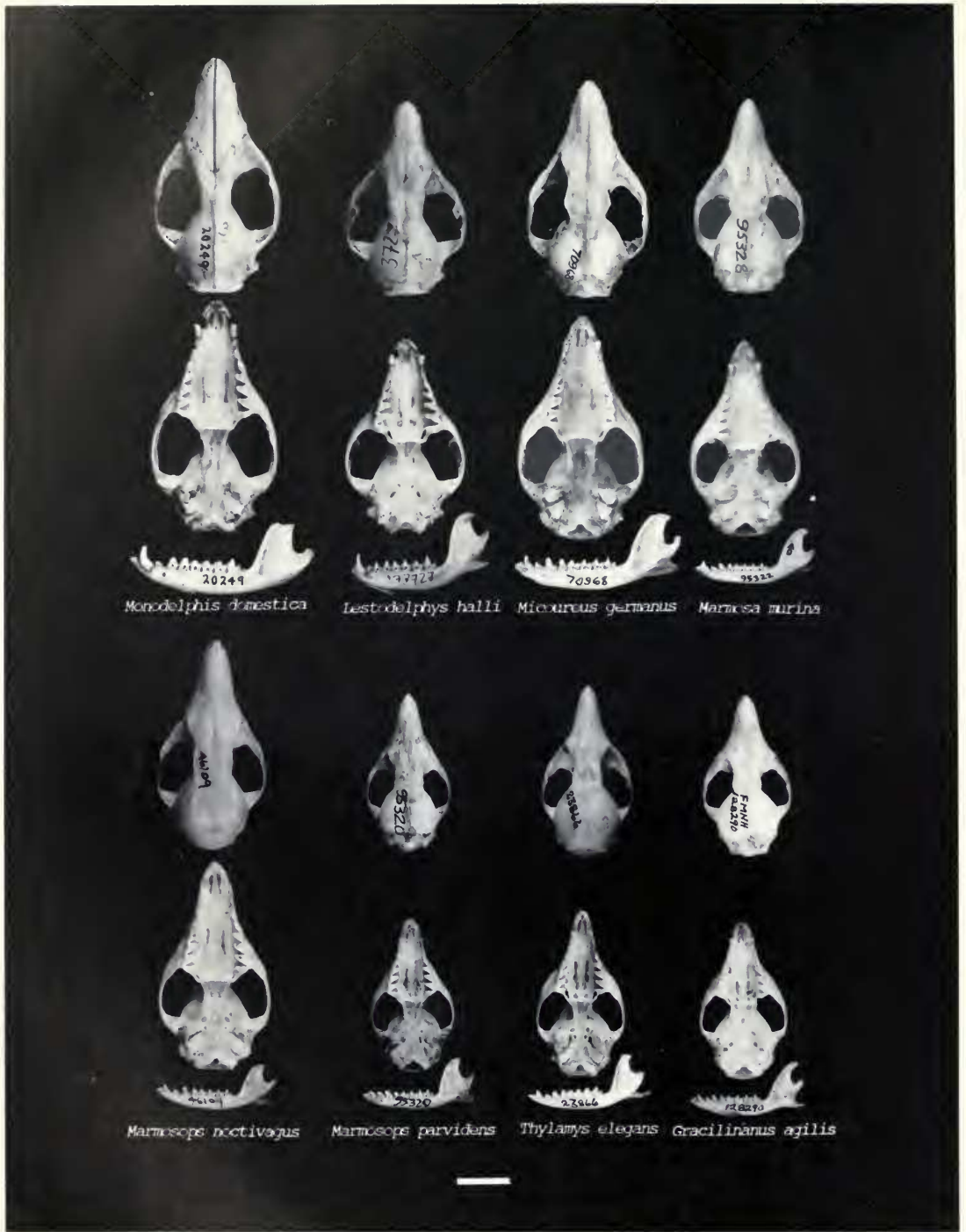


FIG. 8. Skulls of Marmosidae (dorsal and ventral aspects; left mandibles, lateral aspect): *Monodelphis domestica* (FMNH 20249, ♀); *Lestodelphys halli* (MVZUC 173727, ♂); *Micoureus germanus* (FMNH 70968, ♀); *Marmosa murina* (FMNH 95328, ♂); *Marmosops noctivagus* (FMNH 46109, ♂); *Marmosops parvidens* (FMNH 95320, ♀), mandible (FMNH 95322); *Thylamys elegans* (FMNH 23866, ♂); *Gracilinanus agilis* (FMNH 128290, ♂). White bar = 1 cm.

As perceived by Archer (1984, p. 589, fig. 5) "in the juvenile, the palate is entire (i.e., imperforate). In the adult it is fenestrated (perforated) by a large opening between the maxillary and palatine bones. This suggests, with other evidence, that the perforate palate of the marsupial is a secondary feature, not a plesiomorphic synapsid-like condition." The basicranium of a nearly completely developed individual of *Dasyurus geoffroyii* with palate entire is shown by Archer alongside that of an adult with incomplete palate. In material at hand, the palate of adult *Dasyurus* varies from entire to more perforate than that of Archer's model. Comparable variability prevails in *Myrmecobius*, *Petaurus*, *Dactylopsila*, *Pseudocheirus*, *Macropus*, and others. The young of marsupials are born before palatal ossification is complete. In the newborn *Didelphis virginiana*, the skeletal system "is almost entirely in the cartilaginous and membranous stage (McCrary, 1938, p. 198). The degree of palatal perforation in the adult reflects the stage at which ossification was arrested, and not the reverse, as suggested by Archer. Evolution of the hard or bony palate of mammals is nearly completely demonstrable stage by stage in the palates of adult American marsupials, as described above.

Auditory Bulla (figs. 10, 11)

The auditory or tympanic bulla is the derived dome-shaped housing for the chain of three auditory ossicles suspended within the tympanic or middle ear drum. The *Gracilinanus* auditory bulla, like that of all marmosines, is a partially closed, or tripartite, drum with floor or bottom composed of an assembly of three separated bones. The anterior component is the more or less inflated or bowl-shaped posteromedian tympanic wing of the alisphenoid bone. The posterior component is the pneumatized pars petrosa of the periotic (temporal) bone. The middle bone is the ectotympanic. The first two elements and intervening space form the medial bullar wall. The lateral wall of the bulla is formed by the horseshoe-shaped ectotympanic bone, which bounds the meatus. The tripartite bulla is primitive for marsupials and characterizes all living didelphoids except caluromyids (see following).

Inflation of the alisphenoid tympanic wing of the tripartite bulla may have involved an extension of the anteromedial slope of the bone into a process or strut that straddles the carotid canal and may span the foramen ovale. The strut (see

below) gradually disappears with increased inflation of the tympanic wing of the alisphenoid bone.

In *Caluromys* and *Caluromysiops* (fig. 10), the anterior and posterior components of the bullar floor make broad contact without fusion. They enclose and nearly or quite exclude the ectotympanic bone from the bullar exterior. This is the bipartite bulla formed by junction of the inflated wing of the alisphenoid with the enlarged and inflated pars petrosa, which together complete the floor and nearly completely close the medial surface. The auditory meatus normally remains widely open.

The mastoid portion of the temporal bone complex may add to the posterolateral surface of the bulla in didelphoids. A narrow lamina of the basioccipital bone may enter into formation of the medial bullar wall.

A prebullar model from which the tripartite auditory bulla can be derived would resemble that of a species of the shrew *Crociodura* (Soricidae, Lypotyphla) (fig. 10). The tympanic cavity of this small eutherian is closed by nothing more than the horizontally suspended ectotympanic ring and the transparent membrane it supports on its inner rim. A swollen process at the posteromedian base of the alisphenoid bone adumbrates the inflated anterior wing of the inflated bulla of more advanced insectivores and didelphoids. The pars petrosa of the periotic bone is already bowl-shaped in *Crociodura*, but the cochlear promontory remains fully exposed (fig. 10).

The auditory bulla of the shrewlike *Caenolestoides* is tripartite as in marmosids.

In contrast to the preceding, the entotympanic globular bulla of *Dromiciops*, sole survivor of the order Microbiotheria, is extremely inflated and completely closed except for the auditory meatus (fig. 10). The floor is formed by fusion of the tympanic wing of the periotic, the wing of the alisphenoid, and a third bone, which may or may not be the true homologue of a particular eutherian entotympanic bone, all of which are adventitious. This bone fills medial and ventral gaps between periotic and alisphenoid bones and makes sutural connection with a narrow medial lamina of the basioccipital bone. The ectotympanic bone, exposed in the tripartite bulla, is hidden within the completely formed drum of *Dromiciops* with only a small portion of its anteroventral process visible through the meatus of the prepared skull.

It appeared to Segall (1969, p. 489, 1970, p. 169) that the entire posterior two-thirds of the *Dromiciops* bulla was "entotympanic," and that the ec-

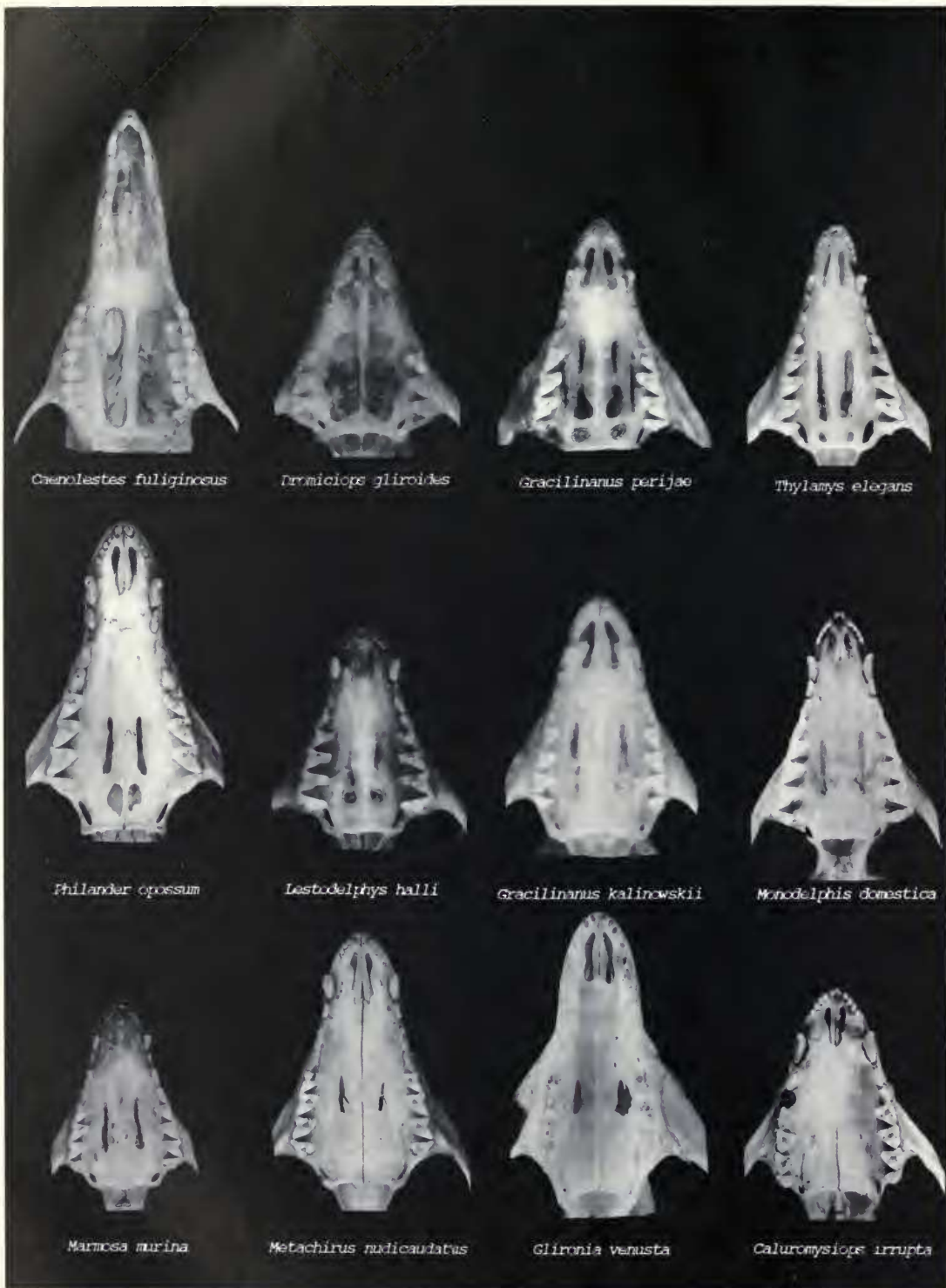


FIG. 9. Palates of American marsupials showing various degrees of ossification, all enlarged to about same palatal width (greatest skull length in millimeters given in brackets): *Caenolestes fuliginosus* (FMNH 79876, ♂ [33.1]); *Dromiciops gliroides* (FMNH 127443, ♂ [28.2]); *Gracilinanus perijae* (USNM 280881, ♂ [28.2], holotype); *Thylamys elegans*

totympanic ring was completely hidden from view. Patterson (1965, p. 7), who may have based his interpretation on the same specimens, but at an earlier date, regarded Segall's "entotympanic" bone on the medial side of the bulla as the tympanic wing of the pars petrosa, and the latter as the inflated pars mastoidea that completes the posterolateral portion of the bulla. Marshall (1982, p. 10, fn.) reviewed the problem without resolution. Reig et al. (1987, pp. 29, 48) followed Patterson without comment. Among some of the 47 skulls of *Dromiciops* before me, nearly the entire margins of the entotympanic bone and pars petrosa are fused. In remaining skulls, the individual sutures marking the entotympanic, alisphenoid, pars petrosa, pars mastoidea, and suture with basioccipital bone are complete and clearly defined externally, each bone except the last well inflated (fig. 10). In one dissected specimen, four chambers of the interior auditory region correspond to the four inflated external bullar bones. An entotympanic bone is present in many eutherians, but among the Marsupialia only in the microbiotheriids *Microbiotherium* and *Dromiciops* does the same bone or its equivalent appear.

Carlsson (1926, p. 252) described and figured a bone identified as entotympanic on the medial side of the bulla in *Dasyuroides*. In specimens examined by me (fig. 10), a hyperinflated alisphenoid bullar component joins with a pars petrosa half the size and an inflated portion of the mastoid bone to complete the drum. An entotympanic bone is not present. According to Kirsch and Archer (1982, pp. 597, 600), who follow Reig et al. (1987, a work then "in preparation"), an entotympanic bone is absent in all marsupials including *Dromiciops* and, by their authority, in *Dasyuroides*.

For all arguments pro and con advanced by Szalay (1982a), Kirsch and Archer (1982), Aplin and Archer (1987), Reig et al. (1987), and Marshall et al. (1990), it has been shown by Hershkovitz (1992) that *Dromiciops*, uniquely characterized by the normal spacing of its four lower incisors (see below), a bifurcated mesopterygoid fossa, closed auditory bulla completed by a distinct component that cannot be other than an entotympanic bone, a short, shallow, rounded symphysis menti, derived didelphoid type astragalus and calcaneus,

and basicaudal cloaca, is the terminal product of a lineage independent of and almost certainly older than that of didelphoids and, by the same tokens, unrelated to Australian marsupials as postulated by Szalay (1982a).

Anteromedian Process or Strut of Tympanic Wing of Alisphenoid Bone (figs. 10, 11)

The strut is present (see above) in all but 3 of about 50 available skulls of *Gracilinanus*. It is clearly absent in each well-rounded bulla of the holotype of *G. kalinowskii* but present in those of the paratype. It is also absent in both bulla of 2 of 39 specimens of *G. agilis* from San Joaquín, Beni, Bolivia. One is an old male (FMNH 114658), the other a juvenile (FMNH 114654) with m³ unerupted. Bullae of the three skulls without strut show no sign of breakage.

Tate (1933) found the strut consistently present in 89 specimens of *Gracilinanus* including those of *emiliae* (1 specimen), *microtarsus* (25), *agilis* (34), *marica* (26), *aceramarcae* (1), minute or incipient in *unduaviensis* (2), and absent in *dryas* (6). He also observed a well-developed process among members of his *elegans* group (*Thylamys*) and *noctivaga* group (*Marmosops*) but none in the *murina* (*Marmosa*) and *cinereus* (*Micoureus*) groups. In FMNH material, the character agrees with Tate's findings except for the three aforementioned *Gracilinanus* specimens. In addition, the strut has been noted in *Lestodelphys*, *Metachirus*, *Philander*, *Chironectes*, and *Lutreolina*, present or absent in *Didelphis*, vestigial or absent in *Caluromys* and *Caluromysiops*, and absent in *Dromiciops*, *Caenolestes*, *Lestoros*, and *Rhyncholestes*. Shape and size of the strut are variable; it may hide the carotid canal from basicranial view and may span or straddle the foramen ovale, the foramen rotundum, or both.

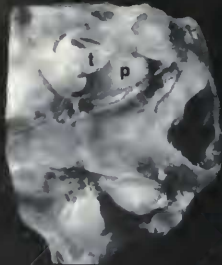
Postcranial Skeleton (tables 2, 3)

The vertebral formula of cervical 7, thoracic 13, lumbar 6, and sacral 2 is plesiomorphic for mam-

←
(FMNH 22333, ♂ [29.6]); *Philander opossum* (FMNH 92297, ♂ [65.1]); *Lestodelphys halli* (MVZUC 173727, ♂ [35.3]); *Gracilinanus kalinowskii* (FMNH 89991, ♀ [24.5], holotype); *Monodelphis domestica* (FMNH 20256, ♀ [38.8]); *Marmosa murina* (FMNH 95328, ♂ [35.3]); *Metachirus nudicaudatus* (FMNH 43172, ♂ [56.7]); *Glironia venusta* (FMNH 41440, ♀ [46.1]); *Caluromysiops irrupta* (FMNH 84426, ♀ [59.0]).



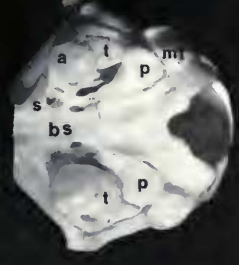
Micoureus germanus



Marmosa murina



Marmosops noctivagus



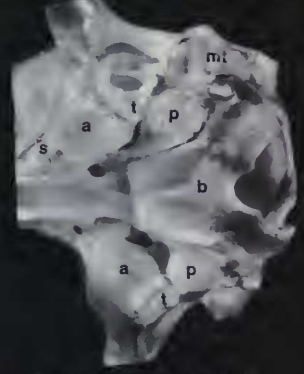
Thylamys elegans



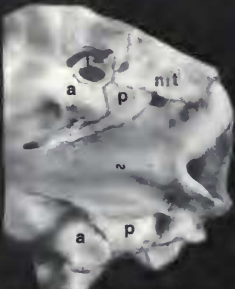
Monodelphis domestica



Glironia venusta



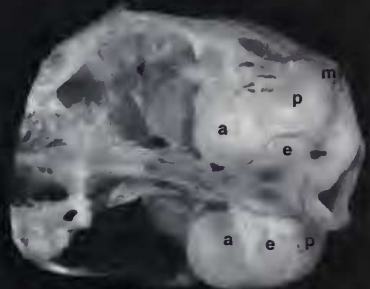
Lestodelphys halli



Caluromys lanatus



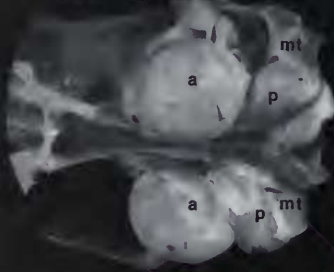
Caluromysiops irrupta



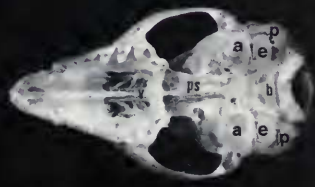
Dromiciops gliroides



Crocidura turta



Dasyuroides byrnei



Dromiciops gliroides

GRACILINANUS

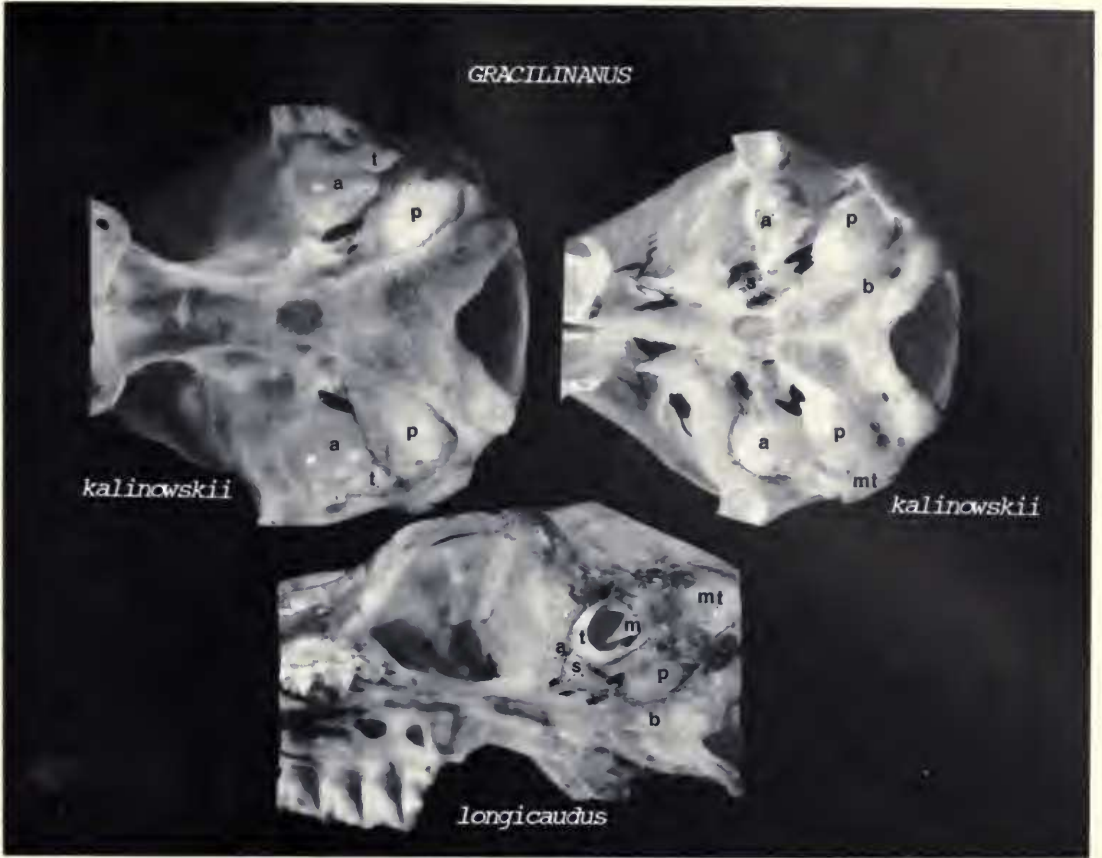


FIG. 11. Tripartite auditory bullae of *Gracilinanus* (not to scale; greatest skull length in millimeters given in brackets): *G. kalinowskii* (FMNH 89991, ♀ [24.5], holotype); *G. kalinowskii* (FMNH 65754, ♀ [24.7], paratype); *G. longicaudus* (FMNH 87924, ♂ [24.8], holotype). a = alisphenoid wing; b = petrous wing; m = malleus; mt = mastoid bone; s = strut or process of alisphenoid wing; t = ectotympanic bone.

FIG. 10. Auditory bullar region of didelphoids, *Dromiciops*, the Australian *Dasyuroides*, and eutherian *Crocidura* (Insectivora) (not to scale; greatest skull lengths in millimeters given in brackets). Upper two rows, tripartite bulla with ventral hiatus between alisphenoid (a) and petrous (p) bones, and fully exposed ectotympanic (t) bone; medial surface with hiatus between alisphenoid and petrous bones. First row: *Micoureus germanus* (FMNH 19635, ♀ [40.5]), *Marmosa murina* (FMNH 95328, ♂ [35.3]), *Marmosops noctivagus* (FMNH 24740, ♂ [37.6]), *Thylamys elegans* (FMNH 23866, ♂ [29.6]). Second row: *Monodelphis domestica* (FMNH 20256, ♀ [38.8]), *Glirionia venusta* (FMNH 41440, ♀ [46.1]), *Lestodelphys halli* (MVZUC 173727, ♂ [35.3]).

Third row: Biparite bulla of *Caluromys lanataus* (FMNH 24142, ♀ [58.8]) and *Caluromysiops irrupta* (FMNH 84426, ♀ [59.0]) with ventral and medial hiati closed by junction of alisphenoid and petrous bones, ectotympanic bone more or less enclosed by drum; global bulla of *Dromiciops gliroides* (FMNH 129804, ♂) with closure of ventral and medial hiati between alisphenoid (a) and petrous (p) bones by "entotympanic" (e) bone, ectotympanic bone enclosed by drum, inflated mastoid (mt) bone forming ventrolateral bullar portion; lamina of basioccipital bone (b) may contribute to dorsomedial bullar surface.

Fourth row: External auditory region of eutherian *Crocidura turba* (Lipotyphla, FMNH 43854 [23.4]), ectotympanic bone (t) with tympanic membrane fully exposed, incipient drum formation with pars periotica (p) and tympanic wing of alisphenoid (a) partially inflated; b = basioccipital, bs = basisphenoid, ps = presphenoid; *Dasyuroides byrnei* (FMNH 127359 [43.8]) with closure of medial and ventral hiati by junction of alisphenoid (a) and petrous (p) bones, inflated mastoid (mt) bone included in bullar composition; *Dromiciops gliroides* (FMNH 127440, ♂ [28.9]) basicranium with incompletely ossified palate exposing vomerine (v) bifurcation of nasal cavity continuous with unique presphenoidal (ps) bifurcation of mesopterygoid fossa; note "entotympanic" bone (e).

TABLE 2. Vertebral formulae of Marmosidae.*

Taxon	Thoracic	Lumbar	Caudal
Marmosidae			
Marmosinae			
<i>Gracilinanus marica</i>	13	5	30 [4]
<i>Marmosa robinsoni</i>	12 (3); 13 (4)	5; 6 (3); 7 (3)	29 (2) [5]; 30 [5]; 31 [5]
<i>Marmosa mexicana</i>	12 (3); 13	5; 6; 7	30 [5]; 31 [5]
<i>Marmosa murina</i>	12	7	30 [5]
<i>Marmosops noctivagus</i>	13	6	29 [5]
<i>Micoureus germanus</i>	13	6	31 [4]
Monodelphinae			
<i>Monodelphis domestica</i>	13	6	19 [5]
<i>Monodelphis touan</i>	13	6	19 [6]
Metachirinae			
<i>Metachirus nudicaudatus</i>	12 (3); 13 (3)	6; 7 (3)	27 [4]; 29 [4] (2); 30 [4]
Thylamyinae			
<i>Thylamys elegans</i>	12	6	21 [6]
Lestodelphyinae			
<i>Lestodelphys halli</i>	13	7	22 [4]

* Cervical vertebrae = 7, sacral vertebrae = 2. When sample is more than 1, number is shown in parentheses. Transitional caudal vertebral number in brackets is included in total caudal number.

mals. The number, 19–39, of caudal vertebrae is derived, the primitive number for American marsupials conjectural. The lowest number of caudals in marmosids is 19 in the shrewlike, mainly terrestrial *Monodelphis*; the highest is 31 in *Marmosa robinsoni*. The highest number of caudal vertebrae

in New World marsupials, 36–39, occurs in *Caluromys*. Marmosid limb size and proportions are compared in table 3. Forelimbs of *Monodelphis* may be shortest relative to trunk length, hind limbs of *Lestodelphys* and *Metachirus* longest relative to trunk length.

TABLE 3. Greatest skull length and limb proportions relative to each other and to vertebral trunk length (thoracic + lumbar + sacral vertebrae in straight line).

Taxon	Greatest skull length	Radius	Humerus	Radius	
				Humerus	Tibia
Marmosidae					
<i>Gracilinanus marica</i>	27.8	16	15	106	22
<i>Marmosa robinsoni</i>	35(34–36)4	19.3(18–21)7	19.6(17–23)7	98.5(87–106)7	26.9(25–29)7
<i>Marmosa mexicana</i>	34	20	19	105	28
<i>Marmosa murina</i>	—	19	18	105	27
<i>Marmosops noctivagus</i>	42.9	25	23	109	27
<i>Micoureus germanus</i>	42.5	26	26	100	34
<i>Metachirus nudicaudatus</i>	51, 54	35(30–39)4	36.8(32–42)6	100.5(94–105)4	51.5(44–57)4
<i>Monodelphis domesticus</i>	35	17	18	94	—
<i>Monodelphis palliolatus</i>	41	19	22	86	27
<i>Monodelphis touan</i>	43	20	22	91	27
<i>Lestodelphys halli</i>	36.7	21.2	21.4	99	28.4

Thoracolumbar Flexure (fig. 11)

The humpback posture in walking assumed by a lactating *Marmosa cinerea* was described by Beach (1939, p. 315) as a means for raising the hindquarters to prevent the dangling, sucking young from scraping the substrate, which they do anyway. Once Beach detached the young from the nipples, the unburdened mother, he said, walked with back straightened.

The flexed or curved spine may be a normal marsupial feature, as it is in the embryo. A flexure at the thoracolumbar junction is shown in X ray by Barnes (1977, figs. 1, 13). A spot check of Field Museum-preserved marsupial skeletons with trunk vertebrae in normal articular relationship reveals the same flexure in American and Australian males and females. The trunk of a monotreme, *Tachyglossus aculeata* (FMNH 60905) with vertebrae in normal articular relationship, is strongly arcuate but without noticeable flexure where thoracic and lumbar vertebrae join. The humpback condition is evident in published photographs of live marsupials. The thoracolumbar flexure apparently allows the animal to assume whatever posture or gait may be most convenient or comfortable and gives spring to leaping.

The vertebral flexure is present and functions similarly among rodents and other mammals that hunch when sitting, roll up when lying, or pivot when hopping or running.

Tarsus (fig. 13)

The two patterns of articular facets of ankle joint bones astragalus and calcaneus have been termed

by Szalay (1982a,b) as separate and continuous. In the separate or primitive pattern, two facets of the dorsal surface of the calcaneus meet with the paired facets of the plantar surface of the astragalus. In the continuous pattern, the two primitively separate facets of each bone are coalesced into one. As has been shown by Hershkovitz (1992), the calcaneal pattern is continuous in the Marmosinae, including *Gracilinanus marica* (one specimen), the Caluromyidae, the caenolestid *Rhyncholestes* (one), and microbiotheriid *Dromiciops* (seven). The separate pattern prevails in the calcaneus of all remaining American marsupials. The pattern of the astragalus was separate in all didelphoids examined by Hershkovitz (1992) but found to be continuous in the single available sample of *Gracilinanus marica*, in one of five *Marmosa robinsoni*, and in all seven astragali examined of the metatheriid *Dromiciops*.

Contrary to Szalay (1982a,b), the separate and continuous ankle bone patterns do not mark two monophyletic clades, one exclusively American (Szalay's Cohort Ameridelphia), the other Australian plus the American Microbiotheriidae (Szalay's Cohort Australidelphia). As detailed here and elsewhere (Hershkovitz, 1992), both patterns and intergrades occur among American marsupials. The derived continuous pattern is dominant in Australia, but the separate pattern persists among the Peramelidae, Macropodidae, and perhaps other groups not examined.

Dental Systems (figs. 6-9, 17-19)

The numerical marmosid dental formula for each upper and lower jaw is the primitive didelphoid

TABLE 3. *Extended.*

Femur	Tibia Femur	Radius + humerus Tibia + femur	Trunk (thoracic + lumbar, sacral)	Radius + humerus Trunk	Tibia + femur Trunk
18	122	77	50	62	80
23.4(21-26)7	114.6(111-124)7	76.8(74-80)6	75(65-86)6	52.5(45-60)6	68(59-75)6
25	112	76	77	51	69
23	117	74	70	53	71
28	96	87	81	59	69
30	113	70	81	64	79
49.8(43-54)6	104(100-110)4	69.5(68-71)4	123, 126, 126	62, 55, 55	89, 78, 82
—	—	—	63	—	—
25	108	79	88	46	59
26	104	79	93	45	57
24.5	116	80.5	94	45	86

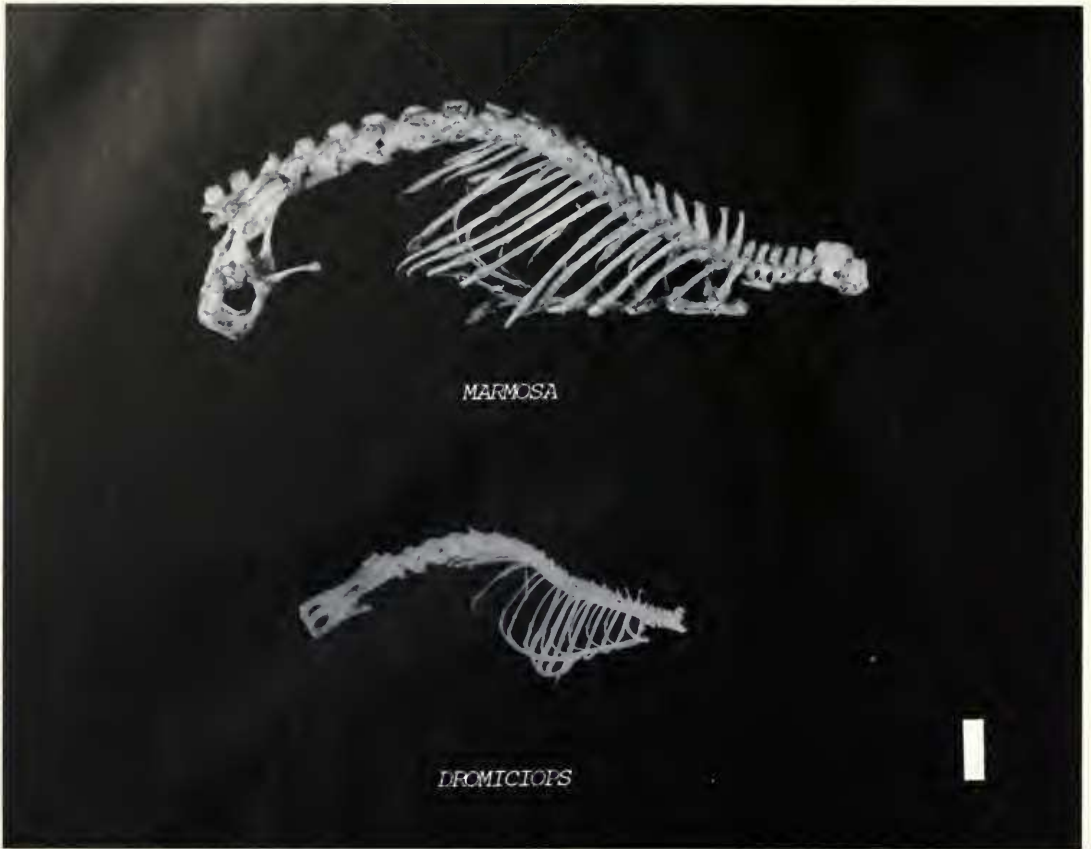


FIG. 12. Thoracolumbar flexure in *Marmosa* (FMNH 124611) and *Dromiciops* (FMNH 127460).

$i_4^5, c_1^1, pm_3^3, m_4^4 = \frac{13}{12} = 50$. The dental morphology is essentially as in didelphoids generally.

All functional adult marsupial teeth are first generation; that is, none is replaced as occurs with the first-generation antemolar teeth of eutherians. The difference in the primitive number between upper and lower incisors in marsupials owes to mandibular contraction with loss of the first lower tooth, thus depriving the first upper incisor of occlusion with a lower equivalent. The phylogenetic numerical incisor formula is, therefore, $\frac{1, 2, 3, 4, 5}{(1), 2, 3, 4, 5}$ (Winge, 1893, p. 122; Hershkovitz, 1982). The morphological numerical formula of the lower suite, 1, 2, 3, 4, is the one universally used but, as in the case of the molars (see below), the phylogenetic notation (1), 2, 3, 4, 5 is preferred. As a rule, lower teeth erupt slightly earlier than their upper counterparts.

Further evidence of mandibular contraction is crowding of the lower incisor alveoli with pinching of the phylogenetic third out of line with incisors

2 and 4. The staggered alveolus of i_3 with buccal buttress is present in all living didelphoids, caenolestoids, all fossil didelphoids known to me with lower incisor field intact, and all polyprotodont Australian marsupials with three lower incisors (Hershkovitz, 1982, in prep.). Progressive reduction in number of mandibular teeth, often accompanied by a compensatory elongation of the anterior incisor as in caenolestids and diprotodont marsupials, ultimately reduces and may eliminate dental crowding and alveolar staggering.

Opossums of the South American order Microbiotheria, with *Dromiciops* its only surviving representative, possess the same incisor formula as didelphoids but with the lower canine smaller and the lower incisors uncrowded, evenly spaced, and in line. This appears to be the primitive metatherian condition.

THIRD PREMOLARS AND FIRST MOLARS—The third upper and lower premolars, the last or penultimate teeth to erupt, have been regarded as sec-

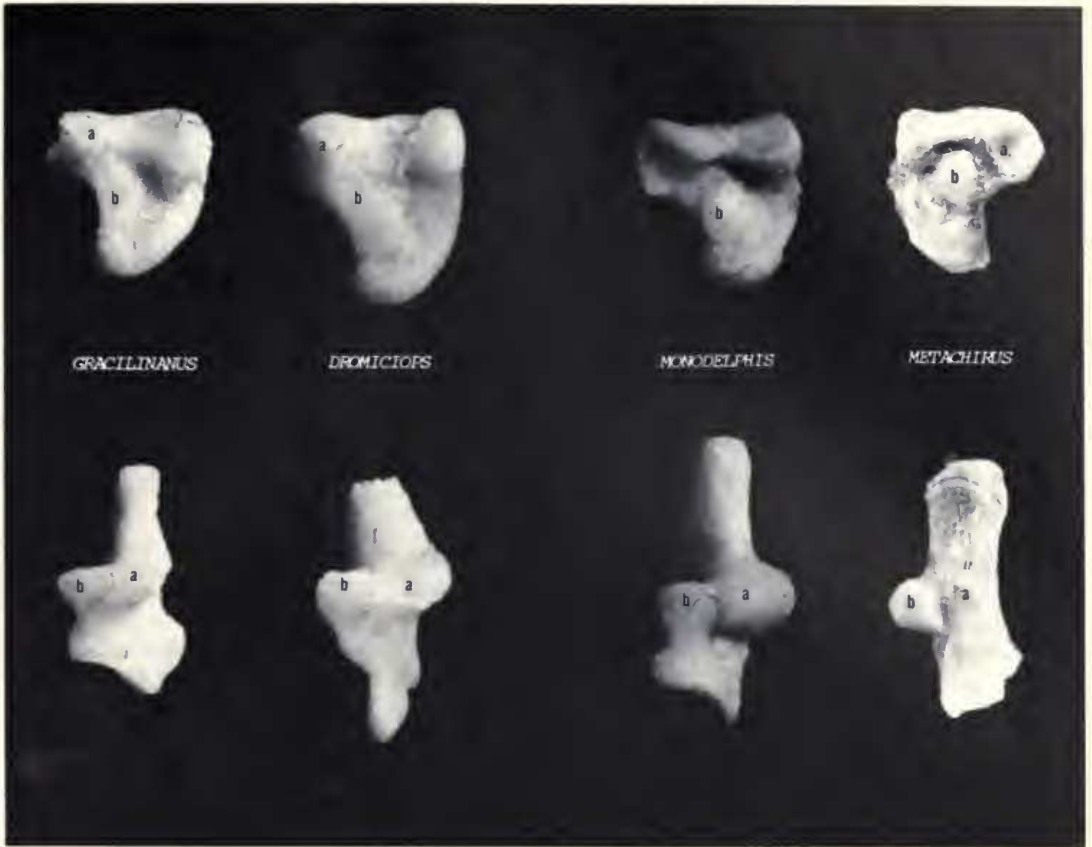


FIG. 13. Astragalus, upper row (plantar aspect), and calcaneus, lower row (dorsal aspect), joint patterns (a, b) (L = left, R = right; not to scale; greatest length given in millimeters): Continuous pattern in *Gracilinanus marica* (FMNH 18107L; astragalus 2.0; calcaneus, 2.6) and *Dromiciops gliroides* (FMNH 50072L; astragalus 1.7; calcaneus 2.8); separate pattern in *Monodelphis palliolatus* (FMNH 22178L; astragalus 2.8; calcaneus, 4.6) and *Metachirus nudicaudatus* (FMNH 70988L; astragalus 5.0; calcaneus, 8.1).

ond-generation successors to deciduous premolars. The so-called marsupial milk premolars, however, are in every sense true molars displaced, not replaced, by the larger, late developing third premolars in the contracted jaws. The laggard third premolar of each jaw develops independently in its own expanding alveolus and in the adult stage dislodges the much smaller more posterior phylogenetic first molar already compacted by the robust fully erupted second molar. The most commonly used serial or morphological formula, 1, 2, 3, 4, for fully erupted upper and lower molars is best abandoned and restated by the phylogenetic adult formula (1), 2, 3, 4, 5. More evidence of jaw contraction is the reduced size of upper and lower last molars. All didelphoid molars are dilambdomorphic and tritubercular.

Bulk of the upper third premolar in the larger species of *Gracilinanus* is generally a fourth or fifth

smaller than that of the second, sometimes subequal, infrequently larger.

SEQUENCE OF ERUPTION—It was shown by Tribe (1990) that eruption of the third premolar precedes that of the last molar (m5) in all species of the family Didelphidae and in *Dromiciops*. In all other American marsupials, including *Gracilinanus*, he found that eruption of m5 precedes that of pm3, with some individual exceptions. Among seven species of *Marmosa* (*canescens*, *mexicana*, *incana*, *murina*, *quichua*, *robinsoni*, *rubra*) only in *robinsoni* was this found variable. The premolar erupted first in one and was intermediate in a second. In *Monodelphis domesticus*, both sequences were represented by the two specimens examined. In *Metachirus*, the premolar erupted first in 18 specimens, was intermediate in 2, followed the last molar in 2, and was ambiguous in 1.

Tribe's terms "dP3" for the deciduous molar,

“P3” for the third premolar, and “M4” for the last molar represent m1 (or dm1), pm3, and m5, respectively.

A spot check of material in the Field Museum supports Tribe’s findings, but the sequence of eruption in *Dromiciops* does not coincide entirely with that of didelphids (*sensu stricto*). In 11 specimens of *Dromiciops* with incompletely erupted third premolars or last molars, eruption of pm³ precedes that of m⁵ in six individuals, in one m⁵ erupts first, and status is indeterminable in four. The last upper molar of *Dromiciops*, it must be noted, is reduced, nearly obsolete. In mandibles of the same specimens, the sequence is reversed. Eruption of m₃ precedes that of pm₃ in nine individuals and erupts at about the same time in two. The difference between times of eruption is slight. Evidently, patterns of dental eruption in *Dromiciops* and didelphids obey different codes. Tribe (1990, p. 568) himself adverted in connection with *Caluromys* that a small or missing m⁵ is “not a case of *Didelphis* pattern of tooth eruption, rather one of suppression of the last molar.”

Cytogenetics

Karyotypes for *Gracilinanus* are unknown. Among the Marmosinae, the diploid number 14 has been recorded for all *Marmosops*, *Micoureus*, and *Marmosa* examined except for a 2n = 22 karyotype in *Marmosa canescens*. The chromosome complements recorded for American marsupials (cf. Hayman, 1990) fall into the following groups. Unless otherwise indicated, all species of the families or subfamilies of each group are presumed to possess the same karyotype.

2n = 14	2n = 18	2n = 22
Marmosidae	Marmosidae	Marmosidae
Marmosinae (part)	Monodelphinae	Marmosinae (part) (<i>Marmosa canescens</i> only)
Thylamyinae		
Metachirinae		
Lestodelphyinae		Didelphidae
Caluromyidae		
Caenolestidae		
Microbiotheriidae (male mosaic with 2n = 13 in somatic tissue [Gallardo and Patterson, 1987])		

Engstrom and Gardner (1988) recorded the diploid number 22 in a male and female each of two subspecies of the Mexican *Marmosa canescens*. In their opinion, the number “probably is independently derived from a primitive 2n = 14 karyotype and is convergent on that of other didelphids,” in this case the Didelphidae.

Sexual Dimorphism

Marsupial males are conspicuously larger than females of the same age. The greater size extends to all parts, including cheiridia, skull, and bony excrescences for support of heavier masticatory muscles. The gular gland is well developed in mature males and smaller, inconspicuous, or absent in females.

Sex Ratios (table 4)

The largest single series of *Gracilinanus* examined is that of *G. agilis* from San Joaquín, Beni, Bolivia. The 32 individuals collected from 2 May through 22 July 1964, by M. L. Kuns, sort into 14 males and 18 females.

Of a total of 297 individuals of marmosine and thylamyine opossums from 32 localities, each represented by 4 or more specimens in the Field Museum collections (table 4), 152 are male and 145 are female. Males preponderate in 15 of the localities, females in 14, and neither in 3. In the 12 localities with 9 or more individuals, males preponderate in 8, females in 3, and neither in 1. In general, males are slightly more numerous than females but not much over the 1:1 sex ratio expected at birth. Males, being larger and unencumbered by attached young, may have a higher survival rate in nature. They also wander over greater distances and are more exposed to capture or predation. Nevertheless, they maintain a positive sex ratio bias.

Age

Fully mature didelphoids are those with the phylogenetic fifth molar and third premolar completely erupted. Either tooth may complete emergence slightly before or after the other. In marmosids, m5 precedes pm3. Juvenals retain the phylogenetic first or deciduous molar, which when shed is never replaced, its comparatively small

TABLE 4. Sex ratios of adult mouse opossums (Marmosinae, Thylaminae) from 32 localities, each with four or more individuals. All specimens in the Field Museum of Natural History. Taxonomic arrangement is alphabetic.

Taxon	Locality	♂♂/♀♀
<i>Gracilinanus</i>		
<i>agilis</i>	San Joaquín, Beni, Bolivia	14/18
<i>Marmosa</i>		
<i>chapmani</i>	Trinidad	8/8
<i>mexicana</i>	Escobas, Izabal, Guatemala	4/2
<i>mexicana</i>	Parque Braulio Carrillo, Heredia, Costa Rica	3/2
<i>murina</i>	Finisanti, Brokopondo, Suriname	7/4
<i>murina</i>	Lelydorppan, Suriname	0/4
<i>robinsoni</i>	Las Marimondas, Valledupar, Colombia	8/1
<i>robinsoni</i>	Pueblo Bello, Cesar, Colombia	3/4
<i>robinsoni</i>	San Jerónimo, Antioquia, Colombia	1/5
<i>robinsoni</i>	Sierra Negra, Valledupar, Colombia	18/11
<i>robinsoni</i>	Unguía, Chocó, Colombia	1/8
<i>robinsoni</i>	Valdivia, Antioquia, Colombia	1/4
<i>robinsoni</i>	Villa Arteaga, Antioquia, Colombia	2/5
<i>robinsoni</i>	Vilanueva, Valledupar, Colombia	18/8
<i>rubra</i>	Río Mecaya, Putumayo, Colombia	7/2
<i>simonsi</i>	Malacates, Tumbes, Peru	7/4
<i>simonsi</i>	Tumbes, Tumbes, Peru	1/3
<i>simonsi</i>	Matapalo, Tumbes, Peru	2/2
<i>Marmosops</i>		
<i>impavidus</i>	Canchaque, Huancabamba, Peru	1/3
<i>impavidus</i>	Pitalito, Huila, Colombia	4/1
<i>impavidus</i>	San Adolfo, Huila, Colombia	4/1
<i>noctivagus</i>	Tres Troncos, Caquetá, Colombia	10/5
<i>Micoureus</i>		
<i>constantiae</i>	Buena Vista, Santa Cruz, Bolivia	3/2
<i>germanus</i>	Tres Troncos, Caquetá, Colombia	1/7
<i>phaeus</i>	Charguayaco, Cauca, Colombia	3/1
<i>phaeus</i>	Sabanetas, Cauca, Colombia	4/4
<i>phaeus</i>	San Adolfo, Huila	5/8
<i>phaeus</i>	San Agustín, Huila, Colombia	3/1
<i>rapposa</i>	Hacienda Cadena, Cuzco, Peru	1/3
<i>Thylamys</i>		
<i>elegans</i>	Concepción, Tucumán, Argentina	1/6
<i>elegans</i>	Olmuc, Valparaiso, Chile	6/5
<i>pallidior</i>	Jesús, Arequipa, Peru	1/3
Total 15 species	32 localities	(Sample total, 297) 152/145 = 1.05/100

alveolar space being preempted by the considerably larger, late erupting third premolar.

Growth appears to be continuous throughout life. Few individuals survive from one breeding season into the next; fewer still survive through two seasons. The different crops are distinguishable by size. The rare 2- or 3-year-old is gigantic compared to 1-year-old conspecifics.

Species Groups of *Gracilinanus*

The nine recognized species of *Gracilinanus* sort into three groups (figs. 6, 7; table 5).

1. *G. agilis* Group

Size large, GSL (adult males and females) 25 mm or more; superior borders of frontal bones little divergent or nearly parallel-sided; weak or spinelike postorbital processes usually present in *G. agilis*; premaxillary symphysis angular; palate with maxillary vacuities present, length of upper molar row (m^{2-5}) 5.1 mm or more; underparts of body not sharply defined white; T to H&B less than 160:100. Included species are *aceramarcae*, *agilis*, *dryas*, *emiliae*, *marica*, *microtarsus*, and *perijae* (new).

REMARKS—Differences between the species are

low grade. Outstanding is the long-haired nearly uniformly brownish *G. dryas*, sympatric with *G. marica*. *G. emiliae* may be sympatric with *G. agilis* in northeastern Brazil. The holotype of *emiliae* is a juvenal, its published measurements misleading for size. *G. agilis* and *G. microtarsus* are parapatric. *G. aceramarcae* is known from the holotype only. The skull of *G. perijae* is narrow and flat. *Gracilinanus* sp. (new species), represented by a very young individual with white underparts, belongs here on size but otherwise is unrelated.

2. *G. longicaudus* Group

Size small, GSL of adult male less than 25 mm; superior borders of frontal bones nearly parallel-sided; premaxillary symphysis acutely angular; palate with maxillary vacuities present; length of upper molar row of adult male 5.1 mm; underparts of body sharply defined white, the hairs self-colored; T to H&B more than 150:100 (164:100, one specimen).

REMARKS—The only known species of the group is a small version of the *G. agilis* morph. T relative to H&B is extremely long, suggestive of the proportionately longer tail of juvenal marmosines.

3. *G. kalinowskii* Group

Size small, GSL of two females less than 25 mm; superior borders of frontal bones strongly divergent; palate with maxillary vacuities absent; length of upper molar row (two females) less than 5.0 mm; underparts of body sharply defined white, the hairs self-colored; T to H&B less than 150:100.

REMARKS—Important characters of the only species of the group are inconsistent with those ascribed to the genus. With characters of the male as yet unknown, the true systematic position of the species remains moot.

Species Accounts

The species are described or discussed in alphabetical order. Only the three species described as new are formally characterized. Representatives of two species, *G. aceramarcae* and *G. emiliae*, were not seen, their characters known to me from the literature only. Characters of the remaining species are mentioned in the generic descriptions, particularly in the section “Variation and Com-

parisons” and in comparisons with the described forms.

Geographic variation among the recognized species is not significant in the material at hand. The subspecies recognized by Tate (1933) have since been sunk by a stroke of the pen by Gardner and Creighton (1989); however, a number may be valid. Pending examination of types, they are simply listed as junior synonyms of the earlier nominate forms.

Gracilinanus aceramarcae Tate

Marmosa aceramarcae Tate, 1931, p. 12. Tate, 1933, p. 202, pl. 11, fig. 101 (skull), pl. 24, fig. 223 (skull)—BOLIVIA: holotype only. Goodwin, 1953, p. 226—holotype history.

Gracilinanus aceramarcae Gardner and Creighton, 1989, p. 5—taxonomy.

HOLOTYPE—Young adult female, skin and skull, AMNH 72568; collected 26 May 1926, by G. H. H. Tate.

TYPE LOCALITY—Río “Aceramarca” (= Acero-marca), Río Unduavi, Yungas, La Paz, Bolivia, 3293 m.

DISTRIBUTION—Known from type locality only (fig. 1).

CHARACTERS—See “Variation and Comparisons” (pp. 9–31).

MEASUREMENTS—See table 5.

REMARKS—Known from holotype only.

SPECIMENS EXAMINED—None.

Gracilinanus agilis Burmeister (figs. 2, 4, 8)

Didelphis murina Lund (not Linnaeus), 1839, p. 233—BRAZIL: *Minas Gerais* (Rio das Velhas). Lund, 1841, pp. 51, 52, 106, 107, 134, 237, 265, 293—

BRAZIL: *Minas Gerais* (Lagôa Santa). Lund, 1842, p. 135—BRAZIL: *Minas Gerais* (Lagôa Santa).

Didelphis pusilla Lund (not Desmarest), 1839, p. 233—BRAZIL: *Minas Gerais* (Rio das Velhas). Lund, 1841, pp. 106, 134, 237, 265, 293—BRAZIL: *Minas Gerais* (Lagôa Santa). Lund, 1842, pp. 133, 199—BRAZIL: *Minas Gerais* (Lagôa Santa).

Grymaeomys pusillus Winge (not Desmarest), 1893, p. 27—BRAZIL: *Minas Gerais* (Lagôa Santa); characters.

M[armosa] pusilla Thomas (not Desmarest), 1900, p. 549—part, BRAZIL: *Minas Gerais* (Lagôa Santa); *agilis* Burmeister, a synonym.

Didelphis elegans Lund (not Waterhouse), 1840, pp. 312, 315—BRAZIL: *Minas Gerais*; *murina* Lund (not Linnaeus), a synonym. Lund, 1842, pp. 133, 135, 199—BRAZIL: *Minas Gerais* (Lagôa Santa).

Marmosa elegans Miranda Ribeiro (not Waterhouse),

TABLE 5. Genus *Gracilinanus*: Measurements (in mm) of recognized species.

Taxon	Sex	Locality	Head and body	Tail	Tail		Ear	Greatest skull length
					Head and Body x 100	Tail		
<i>kalinowskii</i> ¹	♀	Hda. Cadena, Peru	89	117	131	16	18	24.5
<i>kalinowskii</i>	♀	Chanchamayo, Peru	91	110	121	15	15	24.7
<i>longicaudatus</i> ²	♂	Los Micos, Colombia	87	143	164	16	16	24.8
<i>agilis</i> ³	♂	Tingo Maria, Peru	91, 75	136, 122	149, 163	16, 14	18, 15	26.3, 24.5
<i>agilis</i>	♂♂	San Joaquín, Bolivia	106(87-130)10	127(115-136)10	120(100-142)10	14(13-16)10	16(13-20)10	27.7(26.3-30.0)8
<i>agilis</i>	♀♀	San Joaquín, Bolivia	93(81-125)13	119(114-135)12	128(104-150)12	14(13-17)13	16(10-18)13	26.1(25.0-28.3)7
<i>agilis</i>	♀	Unguía, Colombia	106	150	144	18	18	27.4
<i>marica</i>	—	Mérida, Venezuela	—	—	—	—	—	27.0, 27.8, 28.9
<i>marica</i>	♂	Turumiquire, Venezuela	105	132	126	17	—	28.0
<i>dryas</i>	♂♂	Bogotá, Colombia	106, 111	145, 145	136, 131	18, 19	19, 19	28.6, 28.7
<i>microtarsus</i>	♂	Teresópolis, Brazil	123	147	119	18	—	29.3
<i>microtarsus</i>	—	Sta. Catarina, Brazil	—	—	—	—	—	—
<i>emiliae</i> ⁴	♂	"Para," Brazil	75	142	189	15	16	23.1
<i>aceramarcae</i> ⁵	♀	Río Aceramarca, Bolivia	83	112	135	16	16	27.5
<i>perijae</i> ⁶	♂♂	Marimondas, Colombia	110, 114	149, 151	135, 132	17, 18	20, 20	28.2, —

Taxon	Zygomatic breadth	Interorbital constriction	Postorbital width	Braincase width	Nasal length	i-m ⁵	m ^{2,5}
<i>kalinowskii</i> ¹	15.0	3.7	7.8	11.3	9.6	11.1	4.7
<i>kalinowskii</i>	15±	3.8	7.1	11.3	9.7	11.6	4.5
<i>longicaudatus</i> ²	13.4	4.3	5.3	10.1	10.0	12.1	5.1
<i>agilis</i> ³	15.0, 13.8	—	6.2, 6.4	10.8, 10.8	—, 9.6	11.1, —	5.9, 6.0
<i>agilis</i>	15.2(13.7-17.5)9	4.7(4.5-5.1)10	6.1(5.3-6.5)9	11.1(10.6-11.5)9	11.3(11.1-12.9)9	13.3(12.3-14.3)10	5.4(5.2-5.7)10
<i>agilis</i>	14.3(13.2-16.1)11	4.4(4.1-4.7)12	6.2(5.7-6.6)9	10.7(10.2-11.3)9	10.1(9.0-10.8)10	12.7(12.2-13.4)12	5.3(5.1-5.6)13
<i>agilis</i>	15.9	4.8	6.6	11.5	11.3	—	5.3
<i>marica</i>	14.3, 14.8, 15.8	5.0, 4.8, 4.9	6.8, 6.5, 6.5	11.7, 10.8, 11.6	11.3	12.1, 12.4, 13.4	5.3, 5.2, 5.1
<i>marica</i>	15.0	4.7	6.5	11.5	11.7	13.7	5.7
<i>dryas</i>	15.2, 15.2	5.2, 5.0	7.8, 7.5	12.0, 11.6	12.7, 13.4	13.6, 13.1	5.4, 5.7
<i>microtarsus</i>	15.8	5.0	6.5	11.8	12.0	14.5	5.9
<i>microtarsus</i>	14.1	4.7	6.9	11.3	14.5	13.4	5.9
<i>emiliae</i> ⁴	12.8	5.3	5.3	10.0	—	—	—
<i>aceramarcae</i> ⁵	—	5.5	—	11.6	11.9	—	—
<i>perijae</i> ⁶	15.7, —	4.6, 4.7	5.0, 5.1	11.1, —	12.0, 11.9	13.0, —	5.5, 5.3

¹ Holotype (FMNH 89991), adult.² Holotype (FMNH 87924), adult.³ Holotype (BM 27.11.268), young of *Marmosa agilis peruana* Tate (measurements from Tate, 1933).⁴ Holotype (BM 9.3.9.10), juvenile of *Marmosa emiliae* Thomas (measurements from Tate, 1933).⁵ Holotype (AMNH 72568), adult of *Marmosa aceramarcae* Tate (measurements from Tate, 1933).⁶ Holotype (USNM 280881), (as others) adult, measurements followed by those of adult paratype.

- 1914 Anexo, 5, p. 48—BRAZIL: *Mato Grosso* (Salto de Sepotuba).
- Didelphys* [(*Grymaeomys*)] *agilis* Burmeister, 1854, p. 139—BRAZIL (type description).
- Marmosa marica* Thomas (not Thomas), 1927, p. 608—PERU: *Huánuco* (Tingo María, 2000 ft); male and female of which the male (no. 1063) became holotype of *Marmosa agilis peruana* Tate, 1931.
- Grymaeomys agilis* Burmeister, 1856, p. 82, pl. 15, fig. 1 (skull), pl. 11, fig. 6 (skull)—BRAZIL: *Minas Gerais* (Lagôa Santa).
- Didelphis agilis* Mohr, 1941, p. 226—type history.
- [*Marmosa*] *agilis* Trouessart, 1898, p. 1241—classification; a synonym of *Marmosa pusilla*.
- Marmosa agilis* Alho, Pereira, and Paula, 1986, pp. 451, 452—BRAZIL: *Distrito Federal* (Parque Nacional de Brasília; Fazenda Agua Limpa); habitat, diet. Mares, Ernest, and Gettinger, 1986, p. 294—BRAZIL: *Distrito Federal* (Fazenda Agua Limpa, Universidade de Brasília; Ecological Reserve, Instituto Brasileiro de Geografia e Estatística); weight; diet; locomotion; habitat. Redford and da Fonseca, 1986, p. 129—BRAZIL: distribution (cerrado; gallery forest; Atlantic forest; “other”). Nitikman and Mares, 1987, pp. 83, 84, 86, 87, 90, 91—BRAZIL: *Distrito Federal* (Fazenda Agua Limpa, 1000 m); habitat (gallery forest); movements; biomass; weights. Mares, Braun, and Gettinger, 1989, pp. 11, 12—BRAZIL: *Distrito Federal* (15–25 km S Brasília); *Goiás* (22 km NE Cristalina); *Mato Grosso* (108–115 km S Poconé); measurements; reproduction.
- Marmosa agilis agilis* Tate, 1933, p. 194, pl. 11, fig. 94 (skull), pl. 24, figs. 215, 216 (skull)—BRAZIL: *Minas Gerais* (Lagôa Santa; Brumado); PARAGUAY: (“V. Clarrica” (probably Villa Rica)); Sapucay; Concepción; Itapé). Vieira, 1955, p. 353 (part)—BRAZIL: *Minas Gerais* (Lagôa Santa; Brumado). Cabrera, 1958, p. 27—classification; synonyms, *chacoensis* Tate, *blaseri* Miranda Ribeiro. Funayama and Pereira Barretto, 1971, p. 263—BRAZIL: *Trypanosoma cruzi* infection.
- Gracilinanus agilis* Gardner and Creighton, 1989, p. 5—taxonomy; synonyms (*beatrice* Thomas, *muscula* Shamel, *formosa* Shamel, *chacoensis* Tate, *buenvistae* Tate, *peruana* Tate, *undaviensis* Tate, *blaseri* Miranda Ribeiro, *rondoni* Miranda Ribeiro). Patterson, 1992, p. 7—BOLIVIA: *Beni* (Reyes, Rio Beni); measurements.
- Marmosa beatrix* Thomas, 1910, p. 502—BRAZIL: *Ceará* (Ipu, type locality); holotype female, skin and skull, BM(NH) 11.4.23.24; collected 15 June 1910, by Emilia Sneath.
- Marmosa agilis beatrix* Tate, 1933, p. 196, pl. 11, fig. 95 (skull), pl. 27, fig. 217 (skull)—BRAZIL: *Ceará* (Ipu; Jua, near Iguatú); *Ceará* (Sierra Ibiapaba).
- [*Grymaeomys*] *beatrix* Matschie, 1916, p. 270—classification.
- Marmosa muscula* Shamel, 1930a, p. 83—ARGENTINA: *Formosa* (type locality Riacho Pilayo, 10 mi NW Km 182); holotype male, skin and skull, USNM 236330; collected 9 August 1920, by Alexander Wetmore; name preoccupied by *Didelphis* (*Marmosa*) *muscula* Cabanis, 1848 [= *Marmosa murina* Linnaeus].
- Marmosa formosa* Shamel, 1930b, p. 311—replacement name for *Marmosa muscula* Shamel, preoccupied. Tate, 1933, p. 232, pl. 13, fig. 120 (skull), pl. 26, fig. 242 (skull)—type only.
- Marmosa velutina formosa* Cabrera, 1958, p. 33—classification. Ologr, 1959, p. 409—ARGENTINA: *Formosa* (Ingeniero Juárez); characters.
- Marmosa agilis buenvistae* Tate, 1931, p. 10—BOLIVIA: *Santa Cruz* (type locality, Buena Vista); holotype female, skin and skull, BM(NH) 26.12.4.91, collected 7 March 1916, by J. Steinbach. Tate, 1933, p. 197, pl. 11, fig. 97 (skull), pl. 24, fig. 219 (skull)—BOLIVIA: *Santa Cruz* (Buena Vista; Lago Balzón; Puerto Suárez; Sara Province).
- Marmosa agilis chacoensis* Tate, 1931, p. 10—PARAGUAY: *Chaco* (type locality, Sapucay); holotype male, skin and skull, BM(NH) 4.1.5.48, collected 11 September 1903, by W. Foster. ARGENTINA: *Chaco* (Las Palmas); BOLIVIA: *Tarija* (Villa Montes incorrectly cited as from Argentina). Tate, 1933, p. 196, pl. 11, fig. 96 (skull), pl. 24, fig. 218 (skull)—PARAGUAY: (Sapucay; Itapé Camp, near Sapucay); ARGENTINA: *Chaco* (Las Palmas). Massoia and Fornés, 1972, p. 71—ARGENTINA: *Buenos Aires*; *Formosa*; *Chaco*; *Misiones*; *Entre Ríos*. Wainberg et al., 1979, p. 33—ARGENTINA: *Entre Ríos* (Delta del Paraná); karyotype (2n = 14). González, 1985, p. 1—URUGUAY: *Río Negro* (Río Uruguay nr. Fray Bentos—Puerto Unguê; Bopicuá, Río Uruguay; Arroyo Bopicuá).
- Marmosa agilis peruana* Tate, 1931, p. 11—PERU: *Huánuco* (type locality, Tingo María, 2000 ft); holotype “young adult” male, skin and skull, BM(NH) 27.11.1.268; collected 20 January 1927, by R. W. Hendee. Tate, 1933, p. 198, pl. 11, fig. 98 (skull), pl. 24, fig. 220 (skull)—PERU: *Huánuco* (Tingo María, Río Huallaga); *Cajamarca* (Bellavista, Río Marañón valley, 5°30'S, 1000 ft altitude, “probably but not certainly distinct”).
- Marmosa agilis peruania* [sic] Tate, 1933, pl. 11, fig. 98—misspelling.
- Marmosa agilia* [sic] *peruania* [sic], Cabrera, 1958, p. 28—misprints in synonymy of *Marmosa agilis peruana* Tate.
- Marmosa undaviensis* Tate, 1931, p. 11—BOLIVIA: *La Paz* (type locality, Pitiguaya, Río Unduavi, 5800 ft); holotype male, skin and skull, AMNH 72563; collected 12 May 1926, by G. H. H. Tate. Tate, 1933, p. 201, pl. 11, fig. 100 (skull), pl. 24, fig. 220 (skull)—BOLIVIA: *La Paz* (Pitiguaya).
- Marmosa blaseri* Miranda Ribeiro, 1936, pp. 361, 373—BRAZIL: *Goiás* (type locality, San Bento); holotype, skin and skull, Museu Nacional, Rio de Janeiro, no. 1250, purchased 1929 from Sr. José Blaser. Vieira, 1955, p. 352—BRAZIL: *Goiás* (Cana Brava, Nova Roma). Ávila Pires, 1968, p. 164—type history; type locality of lectotype.
- Thylamys rondoni* Miranda Ribeiro, 1936, pp. 385, 387—BRAZIL: *Mato Grosso* (type localities, Salto de Sepotuba and São João de Serra do Norte); types in alcohol, skulls out, Museu Nacional, Rio de Janeiro.
- Marmosa rondoni* Vieira, 1955, p. 352—listed.

HOLOTYPE—Young adult, sex undetermined, skin mounted, Zoologisch Museum, Halle, no. 147; collected by H. Burmeister (cf. Mohr, 1941, p. 226).

TYPE LOCALITY—Lagoa Santa, Minas Gerais, Brazil, 760 m.

DISTRIBUTION (fig. 1)—Tropical and subtropical wooded parts of South America from the Colombian–Panamanian border at the Golfo de Urabá south into low altitudes of central Andean Peru, upper Amazonian and Río Paraná basins of Bolivia, Paraguay, the Río Paraná basin of Argentina, Uruguay, Brazil, and in northeastern and central Brazil, the states of Maranhão, Ceará, Goiás, Minas Gerais, and Distrito Federal; altitudinal range from near sea level to between 500 and 800 m above in the Peruvian Andes and up to 1000–1200 m in the dry forest within the Brazilian cerrado.

The geographic range of *Gracilinanus agilis* is the most extensive and ecologically varied of the genus if not of the family Marmosidae. Yet, the species is unknown from the larger part of South America embraced between its known eastern and western distributional records. It is absent from Venezuela, the Guianan countries, the Orinoco basin of Colombia, and coastal Brazil east and north of the Rio São Francisco. It may be present but has not been recorded from Ecuador, the Amazonian basin except its upper reaches in northeastern Peru and southern Brazil. Presence of *G. agilis* in northwestern South America on the Colombian side of the border, but not the Panamanian side, may be an artifact of collecting.

CHARACTERS—See “Variation and Comparisons” (pp. 9–31).

MEASUREMENTS—See tables 5 and 6.

REMARKS—The range of *Gracilinanus agilis* is more extensive than that of any other species of the genus. Material at hand shows a corresponding wide range of geographic variation but is woefully inadequate for assessment of inter- and intrapopulation variation. The study specimens from a total of 11 localities include 1 from each of 8 localities, 2 from each of 2 localities, and 32 from San Joaquín, Beni, Bolivia, represented by 20 skins with skulls and 12 skulls only.

The San Joaquín series consists of three specimens (2 ♂, 1 ♀) larger in nearly all dimensions and with more uniformly saturate ochraceous underparts than appears in others of the series. Cranially, the lambdoidal crest of the two large males is well developed (absent in others), and in all three the mesopterygoid fossa is narrower, the sides convergent (wider, nearly parallel-sided in the others). The second premolar smaller than the third in the males is larger in the females as in the members of the larger series.

The differences between the two groups may be

TABLE 6. Cranial and dental measurements of the three largest individuals of *Gracilinanus agilis* from San Joaquín, Beni (2 ♂, 1 ♀), Bolivia, compared to remaining members of series and pair of *G. agilis* from Brasília, Distrito Federal, Brazil.

	Greatest skull length	Zygomatic breadth	Interorbital	Braincase width	Nasal	Palate	i-m ⁵	m ²⁻⁵
San Joaquín								
♂♂	27.6, 29.9	16.3, 17.5	4.9, 5.1	11.0, 11.2	11.1, 12.6	14.5, 15.6	13.4, 13.8	5.6, 5.7
♂♂	27.1(26.3–28.7)6	15.0(14.7–16.2)6	4.7(4.5–4.8)8	11.1(10.8–11.5)7	11.5(10.6–12.9)7	14.4(13.8–15.1)8	13.2(12.8–13.6)8	5.3(5.2–5.6)8
♀	28.3	16.1	4.7	11.3	11.8	14.6	13.4	5.7
♀♀	25.7(25.0–26.6)6	14.2(13.2–15.9)10	4.4(4.1–4.7)11	10.6(10.2–11.0)8	11.0(9.0–11.2)9	13.7(13.0–14.9)10	12.6(12.2–13.0)11	5.3(5.1–5.6)12
Brasília								
♂	28.8	15.8	4.6	11.2	13.0	14.7	13.9	5.8
♀	27.4	15.7	4.7	11.7	11.2	14.9	13.2	5.6

significant. On the other hand, few marmosids live beyond their first year. Those of the same population that do are significantly larger, their coloration usually more saturate, and male skulls more robust. Complicating factors include seasonal variation in pelage and coloration and sexual dimorphism, the males averaging larger in all dimensions than females of the same generation. Karyotypes and other nonphenotypic characters are unknown for any gracile mouse opossum. Guided by these considerations, all San Joaquín material is treated as representative of one highly variable species. Measurements of the entire series are shown in table 5. Measurements of the large and small groups compared with each other and with a pair from Brasília regarded as typical *agilis* are shown in table 6.

The adult male and female from Brasília grade into the San Joaquín series except for longer (winter) pelage with dark hair bases of underparts more extensive and showing through. Cranially, the two are intermediate between the large and small San Joaquín series. The individual from Unguía, Colombia, at the northern extreme of the range has upper parts and sides like those from Brasília, but with underparts paler, as in the San Joaquín mouse opossums.

Specimens from a cluster of northeastern Brazilian localities (Jua, Ipiaba, Cocos, Alto Rio Parnahyba), all determined by Tate (1933) as *G. agilis beatrix* Tate, grade into each other as well as with the San Joaquín series, which may be the *G. a. buenavistae* of Tate. At the other extreme of the range, the Field Museum specimens from Nueva Italia in the Paraguayan Chaco, which could be referred to Tate's *G. agilis formosa* or *G. agilis chacoensis*, also agree with the San Joaquín material, as do remaining specimens assigned to the species.

SPECIMENS EXAMINED—44 (FMNH). BRAZIL: Ceará, Jua, 2; Ipiaba, 1; Maranhão, Cocos, 1; Alto Rio Parnahyba, 1; Distrito Federal, Brasília, 2; BOLIVIA: Beni, San Joaquín, 32; Oruro, Mt. Sajama, 1; Santa Cruz, Santiago, 1; Tarija, Tablada, 1; PARAGUAY: Chaco, Nueva Italia, 1; COLOMBIA: Choco, Unguía, 1.

Gracilinanus dryas Thomas

Marmosa dryas Thomas, 1898, p. 456. Tate, 1933, p. 203, pl. 11, fig. 102 (skull), pl. 24, fig. 224 (skull)—VENEZUELA: Mérida (Selva Culata, 4000 m; Montañas Uchisera, 3000 m; Montes de la Sierra). Handley, 1976, p. 6—VENEZUELA: Mérida (Ta-

bay); Táchira (Buena Vista); Trujillo (Hacienda Misisí). Handley and Gordon, 1979, p. 67—COLOMBIA: Cundinamarca (Boquerón de San Francisco, Bogotá); VENEZUELA: Mérida (Mérida; Uchisera); Tabay; Culata; Montes de la Selva; Uchisera); Táchira (Buena Vista); Trujillo (Hacienda Misisí). Pérez-Hernández, 1989, p. 369—VENEZUELA: Táchira (Betania, Distrito Junín); Trujillo (13–15 km E Trujillo); altitudinal range 2210–4000 m.

[*Grymaeomys*] *dryas* Matschie, 1916, p. 270—listed. *Gracilinanus dryas* Gardner and Creighton, 1989, p. 6—taxonomy.

HOLOTYPE—Old adult male, skin and skull, BM(NH) 98.5.15.2; collected 14 December 1896, by Salamón Briceño.

TYPE LOCALITY—Culata, Sierra de Mérida, Mérida, Venezuela, 4000 m.

DISTRIBUTION (fig. 1)—Temperate zone forests of the northern Cordillera Oriental from the latitude of Bogotá, in Colombia, north into the Sierra de Mérida of northwestern Venezuela; sympatric with *Gracilinanus marica*.

CHARACTERS—See “Variation and Comparisons” (pp. 9–31).

MEASUREMENTS—See table 5.

SPECIMENS EXAMINED—2 (FMNH). COLOMBIA: Cundinamarca, Bogotá, Boquerón de San Francisco.

Gracilinanus emiliae Thomas

[?] *Didelphys pusilla* Thomas (part, not Desmarest), 1888, p. 349—part, BRAZIL: Pará (Santarém); “skin of head, skull”; purchased.

Marmosa emiliae Thomas, 1909, p. 379. Tate, 1933, p. 189, pl. 10, fig. 89 (skull), pl. 23, fig. 210 (skull), holotype only. Ávila Pires, 1964, pp. 8, 11—BRAZIL: Amazonas (Km 50, Manaus–Itacoatiara RR).

[*Marmosa*] *Emiliae* Cabrera, 1913, p. 14—classification.

[*Grymaeomys*] *emiliae* Matschie, 1916, p. 270—listed.

Gracilinanus emiliae Gardner and Creighton, 1989, p. 6—taxonomy; *agricolai* Moojen, a synonym. Patterson, 1992—BRAZIL: Amazonas (Codajás, Rio Solimões; Igarapé Grande, Upper Rio Juruá).

Marmosa agricolai Moojen, 1943, p. 2, fig. 1 (skull)—BRAZIL: Ceará (type locality, Crato); holotype male, skin and skull, Museu Nacional, Rio de Janeiro, no. 1495; collected 26 August 1936, by A. Leito de Carvalho. Cabrera, 1958, p. 28—possibly a race of *microtarsus*.

Marmosa microtarsus microtarsus Tate (part not Wagner), 1933, p. 192—BRAZIL: Pará (Santarém); comment on BM specimen recorded as *Didelphys pusilla* by Thomas.

HOLOTYPE—Subadult male, skin and skull,

BM(NH) 9.3.9.10; collected 13 February 1909, by Emilia Sneathlage.

TYPE LOCALITY—"Para," Brazil.

DISTRIBUTION (fig. 1)—Recorded from the middle and lower Amazon basin, and Crato in the arid northeastern coast of Brazil. The holotype is said to be from "Para." This place name may refer to the state of Pará or the Atlantic port town since renamed Belém. Ávila Pires (1964) records *Marmosa emiliae* from between Manaus and Itacoatiara in the state of Amazonas. Thomas (1888, p. 349) mentions a "skin of head, skull" from Santarém, Rio Tapajóz, as *Didelphys pusilla*. Tate (1933, p. 192) refers to the same specimen as "unquestionably *microtarsus*" but shows (1933, p. 187) Santarém outside the range of that species. According to Gardner and Creighton (1989, p. 6), the holotype of *Marmosa agricolai* Moojen from Crato, Ceará, is referable to *Gracilinanus emiliae*.

The specimen from Igarapé Grande, Upper Rio Juruá, and another from Codajás, north bank Rio Solimões, recorded by Patterson (1992) are immature. They may represent undoubted *Gracilinanus emiliae*.

On the basis of the geographic evidence alone, the lower Rio Amazonas individuals recorded by Ávila Pires (1964) and by Thomas (1888) may also be *emiliae*; the *Crato agricolai*, however, is problematic.

CHARACTERS—See "Variation and Comparisons" (pp. 9–31).

MEASUREMENTS—See table 5.

REMARKS—According to Tate (1933, p. 189), the holotype of *emiliae* is a "young adult male, M⁴ [= m⁵] not fully erupted." Handley (pers. comm.), who also examined the holotype, notes that pm³ and m⁵ are not fully erupted, auditory bulla "tiny," teeth "small," and supraorbital region "beaded." He adds that "except for narrower interorb[ital] region] and braincase, the skull is similar to *marica* of like age."

SPECIMENS EXAMINED—None.

Gracilinanus kalinowskii, new species (figs. 2, 6, 7, 9, 11, 14)

HOLOTYPE—Adult female, skin and skull, FMNH 89991; collected 9 July 1958, by Celestino Kalinowski; original number 475.

TYPE LOCALITY—Hacienda Cadena, Marcapata, 13°20'S, 70°46'W, Cuzco, Peru, 890 m.

DISTRIBUTION (fig. 1)—Known only from the tropical and subtropical forested slopes of the An-

Gracilinanus kalinowskii

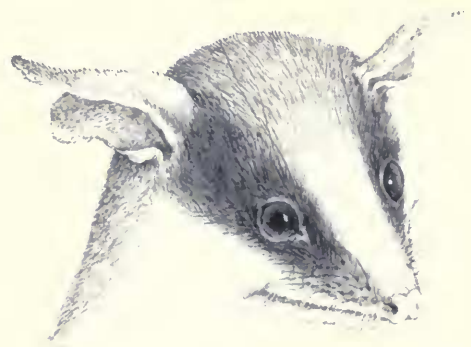


FIG. 14. *Gracilinanus kalinowskii*, portrait.

des and foothills of southeastern Peru from the Department of Junín into that of Cuzco.

ETYMOLOGY—The species is named in memory of Celestino Kalinowski, who discovered the holotype and collected more specimens and species of Peruvian mammals from more localities than anyone else. His collections for the Field Museum of Natural History include 2,748 mammals, the first dated 12 November 1948, the last 17 March 1962.

CHARACTERS—External—Size comparatively small, pelage slightly crinkly, upper parts of body, sides, and outer surface of limbs cinnamon brown; crown like back, muzzle between eyes contrastingly paler; dark brown eye ring extending to base of ears; underparts from chin to anus, ankles, wrists, and sides of body extremely pale, nearly white, the hairs uniformly colored; cheeks like throat; two pairs of pectoral teats present, the mammary formula 7–1–7 = 15; gular gland not evident in cut and stitched area of skin; palmar surface of manus smooth, tubercles separate, pads 1 (thenar), 2, and 3 touching but not united; plantar surface smooth, tubercles separate; claws of forefoot comparatively stout, extending slightly beyond tips of digits; claws of hind foot strongly recurved, extending well beyond digits, tail blotched pale brown, scutal arrangement appears spiral in holotype, annular in paratype, but appreciation may depend on viewer, caudal portion and its condition, or preparation.

Cranial—Skull small; zygomata widely expanded, sides of supraorbital region beaded, widely divergent posteriorly; braincase well rounded dorsally; nasals broadly tapered, the tips rounded; incisive symphysis rounded; palatal vacuities reduced, the maxillopalatine narrow, posteromedial



FIG. 15. *Gracilinanus longicaudus*, portrait.

small, maxillary absent; alisphenoid portion of bulla without sign of anteromedian process or strut.

Dental—Upper incisors extremely worn but apparently subequal in size; lower incisors with alveolar area damaged in preparation but phylogenetic i_3 (second in line) staggered, the alveolus buttressed as in all didelphoids (HersHKovitz, 1982); upper second premolar nearly twice bulk of third; molars extremely small.

MEASUREMENTS—See table 5.

COMPARISONS—Outstanding among distinctive characters are the short, comparatively broad, rounded muzzle tip, widely divergent superior borders of frontals without postorbital process, globular braincase, less perforated palate, absence of anteromedian process or strut of alisphenoidal wing of bulla, small pm^3 little more than half bulk of pm^2 .

The species of *Gracilinanus* compared are *microtarsus*, *marica*, *agilis*, and *dryas*. Two others not seen include *aceramarcae* Tate and *emiliae* Thomas. The first, known from the holotype only, in the British Museum (Natural History), is said to be a “young adult female,” but its badly damaged skull as figured by Tate (1933, p. 202, pl. XI, fig. 101 [dorsal], pl. 24, fig. 233 [ventral]) appears to be that of a juvenal or subadult. Its narrow, pointed muzzle, highly fenestrated palate, narrow zygomata, dark underparts, and overall larger size (table 1) readily separate it from *kalinowskii*.

The holotype of *Gracilinanus emiliae* Thomas, also preserved in the British Museum (Natural History), is described as a juvenal with $m4$ (= $m5$) unerupted. The published measurements mis-

leadingly suggest a small species the size of *G. kalinowskii*. Cranial characters, as described by Thomas (1909, p. 379), and described and figured by Tate (1933, pl. X, fig. 89, pl. XXIII, fig. 210), however, show the pointed muzzle and highly fenestrated palate common to all species of the large-sized *Gracilinanus agilis* group.

REMARKS—The cranial characters of *G. kalinowskii* diverge markedly from those usually attributed to the genus (Gardner and Creighton, 1989, p. 5). The fully mature skull bears a strong resemblance to skulls of young members of the large *Gracilinanus agilis* group with unerupted $m4$ or $m5$. At maturity, the supraorbital borders of the latter become nearly parallel-sided, the braincase less globose to nearly flat, palate perforated as usual.

The paratype (FMNH 65754) of *G. kalinowskii* from Chanchamayo resembles the holotype externally, but with gular gland evident, caudal scales annular, braincase slightly less globular, anteromedian process or strut of alisphenoid portion of bulla present.

SPECIMENS EXAMINED—2 (FMNH). PERU: *Cuzco*, Hacienda Cadena, the holotype; *Junín*, Chanchamayo, 1.

Gracilinanus longicaudus, new species (figs. 6, 7, 11, 15)

HOLOTYPE—Adult male, skin and skull, FMNH 87924; collected 29 April 1957, by Kjell von Sneidern.

TYPE LOCALITY—Los Micos, San Juan de Arama, 03°20'N, 73°53'W, Meta, Colombia, 396 m.

DISTRIBUTION (fig. 1)—Known only from type locality in the Cordillera de La Macarena, eastern slope of the Cordillera Oriental de los Andes, Meta, Colombia.

ETYMOLOGY—The name *longicaudus* refers to what may be the longest-tailed species of the genus.

CHARACTERS—**External**—Size comparatively small, pelage slightly crinkly, upper parts of body cinnamon brown, muzzle between eyes ochraceous orange; blackish eye ring incomplete, without posterior and posteroventral segments; ventral surface from chin to anus, inner side of limbs to wrists and ankles, cheeks pale yellowish nearly white, the hairs uniformly colored; throat gland present, the skin bare; palms, soles, and individually separated pads granular; claws of forefeet and hind feet extending nearly or quite to tips of digits;

tail uniformly brown but with whitish hairs ventrally; bristles more or less uniformly thick, the middle slightly more than two scales long, the laterals shorter; scutular pattern annular.

Cranial—Skull extremely small, elongate, the zygomata little expanded; muzzle pointed, dorsal contour flat, the braincase not inflated. supraorbital region beaded, the sides moderately divergent; palate fenestrated as usual; bulla small but with the alisphenoid strut extending across foramen ovale.

Dental—Upper incisors subequal in size, the fifth slightly smaller than second; second premolar slightly larger than third, buccal and lingual cingula complete in both; molars comparatively large; first in line lower incisor largest of series, second in line (i_2) staggered and buttressed as usual, canine with well-developed posterior cingular style.

MEASUREMENTS—See table 5.

COMPARISONS—*Gracilinanus longicaudus* is the smallest species of those with pointed muzzles, its tail relatively longest, that of *G. emiliae* possibly excepted. Resemblance is nearest *G. marica* but size smaller, tail relatively longer. *G. longicaudus* and *G. kalinowskii* are about the same size, both with underparts whitish, but eye ring of *longicaudus* is incomplete, tail much longer. Cranial differences between the two are those that separate *kalinowskii* from all pointed muzzle species.

REMARKS—Although *G. longicaudus* is represented only by the holotype, the combination of small size, long tail, whitish underparts, incomplete eye ring, and narrow skull separates it from all other described species.

Cranially, *G. longicaudus* resembles most adults of the larger members of the *G. agilis* group but without any of the juvenal-like traits such as those noted in the adult skull of the equally small *G. kalinowskii*.

The extremely long tail relative to head and body (188:100) of *Gracilinanus emiliae* with greatest skull length 23.1 mm is that of a juvenal. It compares with a T:H&B relation of 164:100 with GSL 24.8 of the fully mature holotype *G. longicaudus*. It is virtually certain that the relative tail length of adult *G. emiliae* would be appreciably shorter than that of the young holotype. In an adult of the large species *G. agilis*, T:H&B ranges from 100 to 150:100. That of the youngest *G. agilis* at hand, from Cocos Coda, Maranhão, with GSL 27.8, is 173:100. (See also "Tail Function in Sexual Behavior," pp. 8–9.)

SPECIMENS EXAMINED—1 (FMNH). COLOMBIA: Meta, the holotype.

Gracilinanus marica Thomas (figs. 6, 7, 13)

M[arrosa] pusilla Thomas (not Desmarest), 1896, p. 314—VENEZUELA: Mérida (Sierra de Mérida).

Marmosa pusilla Elliott (not Desmarest), 1907, p. 4—VENEZUELA.

Marmosa marica Thomas, 1898, p. 455—type description. Elliot, 1907, p. 4—VENEZUELA. Tate, 1933, p. 200, fn., pl. 11, fig. 99 (skull), pl. 24, fig. 221 (skull)—VENEZUELA: Mérida (Río Albarregas; Cafetal de Milla; Llano de Mérida; Cafetal de Mérida; Pedregosa); Sucre (Mt. Turumiquire). Handley, 1976, p. 7—VENEZUELA: Distrito Federal (Los Venados; Pico Ávila); Falcón (Urama; Hato Mata de Bejucó). Handley and Gordon, 1979, p. 68 (part)—VENEZUELA: Distrito Federal (Los Venados; Pico Ávila); Falcón (Urama); "Monagas" (Cerro Turumiquire; Hato Mata de Bejucó); Mérida (Cafetal de Chama; Cafetal de Mérida; Cafetal de Milla; Mérida; Río Albarregas). Pérez-Hernández, 1989, p. 369—VENEZUELA: Distrito Federal (Hacienda El Limón); Aragua (Estación Biológica Rancho Grande).

[*Grymaeomys*] *marica* Matschie, 1916, p. 270—listed. *Gracilinanus marica* Gardner and Creighton, 1989, p. 6—taxonomy.

HOLOTYPE—Young adult male, skin and skull, BM(NH) 98.5.15.1; collected 24 January 1897, by Salamón Briceño.

TYPE LOCALITY—Río Albarregas ("Abarregas"), Mérida, Venezuela, 1630 m.

DISTRIBUTION (fig. 1)—Northern Venezuela and northern Colombia from the Caribbean coast of Venezuela west of the Delta del Río Orinoco into the Sierra de Mérida, thence south into the Cordillera Oriental at least to the latitude of Bogotá.

CHARACTERS—See "Variation and Comparisons" (pp. 9–31).

MEASUREMENTS—See tables 5 and 7.

REMARKS—Handley and Gordon (1979, p. 68) recorded without comment three northern Colombian gracile opossums as *G. marica*. Two are the Las Marimondas specimens preserved in the National Museum of Natural History and are described here as *G. perijae*. The third, in the British Museum (Natural History), is from "Silva" (= La Selva, an ancient farm near Bogotá). According to Handley (pers. comm.), the La Selva specimen is a skull only with "braincase inflated" and interorbital region "broad posteriorly." In these respects, the skull, as described, differs significantly from that of *perijae* and agrees with that of *marica* or most other species of the *G. agilis* group.

Gracile opossums recorded from Peru as *Marmosa marica* by Thomas (1927) were later described by Tate (1931, p. 11) as *Marmosa agilis*

TABLE 7. Summary of selected measurements of *Gracilinanus perijae* and *G. marica* (see table 5 for additional measurements).

Taxon	Sex	Locality	Greatest skull length	Postorbital constriction	Postorbital breadth	Braincase width	Braincase height from bulla	m ²⁻⁴	m ²⁻⁵	Source
<i>Gracilinanus perijae</i>	♂♂	Marimondas	28.2, —	4.6, 4.7	5.7, 5.1	11.1, —	8.9, —	4.8, 4.5	5.5, 5.1	This paper
<i>marica</i>	♂♂	Mérida	27.0, 28.9, 28.7	5.0, 4.9, 4.8	6.8, 6.4, 6.3	11.7, —, 11.5	9.5, 9.6, 9.7	4.7, 4.7, 4.8	5.3, 5.1, 5.7	This paper
<i>marica</i>	??	Mérida	27.8, —	4.9, 4.9	5.6, —	11.5, —	9.5, —	4.6, 4.8	5.1, 5.3	This paper
<i>marica</i>	♂♂	Mérida	27.8(27.1–28.5)	5.75(5.5–6.0)	—	11.4(11.1–11.8)	—	4.8(4.7–4.9)	—	Tate, 1933
<i>marica</i>	♀♀	Mérida	25.4, 26.6, 27.1	5.9(5.7–6.1)	—	11.25(11.1–11.6)	—	4.75(4.7–4.8)	—	Tate, 1933

peruana (= *M. agilis*). The immature female, provisionally identified by Lönnberg (1921, p. 70) as "*Marmosa cf. marica*," was redetermined by Tate (1933, p. 178) as *Marmosa cauae* (= *Marmosops cauae* Thomas, 1900).

SPECIMENS EXAMINED—6 (FMNH). VENEZUELA: Mérida, 5; Sucre, Mt. Turumiquire, 1.

Gracilinanus microtarsus Wagner (figs. 1, 3)

Didelphys microtarsus Wagner, 1842, p. 359. Wagner, 1843, p. 43—English translation of original German description. Waterhouse, 1846, p. 512—characters. Wagner, 1850, p. 147—BRAZIL: São Paulo (type locality, Ypanema). Wagner, 1855, p. 243—characters. Pelzeln, 1883, p. 114—part, BRAZIL: São Paulo (Ypanema); characters.

Grymaeomys microtarsus Winge, 1893, p. 24—BRAZIL; characters.

[*Marmosa*] *microtarsus* Trouessart, 1898, p. 1239—as a synonym of *Marmosa murina*.

Marmosa microtarsus Thomas, 1900, p. 549—BRAZIL: Paraná (Palmeira); comparison with *pusilla*. Miranda Ribeiro, 1935, p. 38—BRAZIL: Rio de Janeiro (Teresopolis). Davis, 1947, p. 3—BRAZIL: Rio de Janeiro (Teresopolis); habitat. Wainberg et al., 1979, p. 33—BRAZIL: karyotype (2n = 14). da Fonseca and Kierulff, 1988, pp. 108, 116, fig. 5 (animal)—BRAZIL: Minas Gerais (Rio Doce State Park); habitat; locomotion; movements; measurements. Stallings, 1988, p. 159—BRAZIL: Minas Gerais (Rio Doce State Park); morphometrics.

Marmosa microtarsus microtarsus Tate, 1933, p. 190, pl. 11, figs. 90, 91 (skull), pl. 23, figs. 211, 212 (skull)—BRAZIL: São Paulo (Ypanema); Rio de Janeiro (Porto Real; Rio de Janeiro); Paraná (Palmeira); Santa Catarina (Joinville, near Rio Itapocu; Blumenau; Araranguá). Vieira, 1949 (1950), p. 352—BRAZIL: São Paulo (Piracicaba; Perús; Ipiranga; Ituverava); Rio de Janeiro (Ilha Grande). Vieira, 1955, p. 350—BRAZIL: São Paulo (Ituverava, Piracicaba; Perús, Ipiranga); Rio de Janeiro (Ilha Grande; Terezopolis); Paraná (Palmeira); Santa Catarina (Araranguá; Blumenau; Joinville). Cabrera, 1958, p. 31—classification; *herhardti* Miranda Ribeiro possibly a synonym. Funayama and Pereira Barretto, 1971, p. 263—BRAZIL: São Paulo (Franca); *Trypanosoma cruzi* infection.

Gracilinanus microtarsus Gardner and Creighton, 1989, p. 6—taxonomy (synonyms: *guahybae* Tate, *herhardti* Miranda Ribeiro).

[?] *Marmosa herhardti* Miranda Ribeiro, 1936, pp. 361, 382—BRAZIL: Santa Catarina (type locality, Humboldt); type, skin (skull?) in Museu Nacional, Rio de Janeiro, purchased from W. Erhardt. Ávila Pires, 1968, p. 165—type adult female, skin and skull (Museu Nacional no. 1226) collected 23 December 1915.

Marmosa microtarsus guahybae Tate, 1931, p. 10—BRAZIL: Rio Grande do Sul (Ilha de Guahyba, near Porto Alegre). Tate, 1933, p. 192, fig. 3, p. 35 (mam-

FIG. 16. *Gracilinanus perijae*, portrait.

mae), pl. 11, figs. 92, 93 (skull), pl. 24, figs. 213, 214 (skull)—BRAZIL: *Rio Grande do Sul* (Guahyba Island; Taquara; São Lourenço).

Grymaeomys agilis Hensel (not Burmeister), 1872, p. 123—BRAZIL: *Rio Grande do Sul* (Island in Rio Guahyba, near Porto Alegre).

Marmosa agilis Davis (not Burmeister), 1945, p. 119—BRAZIL: *Rio de Janeiro* (Teresopolis, Fazenda Boa Fé), da Fonseca and Kierulff, 1988, pp. 108, 112, 128, 137—BRAZIL: *Minas Gerais* (Rio Doce State Park); morphometrics.

Marmosa agilis agilis Vieira (part not Burmeister), 1949 (1950), p. 351—BRAZIL: *São Paulo* (Jaboticabal; Ilha Victoria), Vieira, 1955, p. 353—*São Paulo* (Jaboticabal; Ilha Victoria; Ilha de São Sebastião).

Didelphys pusilla Thomas (part not Desmarest), 1888, p. 348—part, not synonymy; BRAZIL: *Rio de Janeiro*; *Santa Catarina*; *Rio Grande do Sul* (Taquara; São Lourenço).

Micoureus pusillus Goeldi (not Desmarest), 1894, p. 462—BRAZIL: *Rio de Janeiro* (Serra dos Orgãos); habits. Ihering, 1894, p. 11—BRAZIL: *São Paulo*.

M[armosa] pusilla Thomas (not Desmarest), 1900, p. 549—BRAZIL: *Paraná* (Palmeira).

[?] *Marmosa pusilla* Shufelt (not Desmarest), 1926, pp. 563, 574, pl. 2, fig. 5 (skinn)—BRAZIL: *Rio Grande do Sul* (São Lourenço).

TYPES—A series of eight specimens, Vienna Museum no. 48; collected January, March, June, and October between 1819 and 1821, by Johann Natterer (cf. Pelzeln, 1883, p. 114). Tate (1933, p. 191) lists only three males but in his table 1 of measurements designates the adult male, “Vienna 48A,” “type,” in this case lectotype.

TYPE LOCALITY—Ipanema (= Ypanema) between São Paulo and Sorocaba, São Paulo, Brazil.

DISTRIBUTION (fig. 1)—Atlantic coastal forests of southeastern Brazil in the states of eastern Minas Gerais, Rio de Janeiro, São Paulo, Paraná, Santa Catarina, and northern Rio Grande do Sul.

Insofar as known, the range of *microtarsus* approaches that of *agilis*, but without indication of overlap or interdigitation. None of the recorded São Paulo specimens has been examined by me or reviewed by others.

CHARACTERS—See “Variation and Comparisons” (pp. 9–31).

MEASUREMENTS—See table 5.

REMARKS—*Gracilinanus microtarsus* as represented here by two skins and five skulls is distinguished from its parapatric ally *G. agilis* by warmer, more reddish dorsal coloration. The slight postorbital process of the nearly parallel-sided interorbital region, a key specific character of *G. agilis*, is also present in *G. microtarsus*. The available data suggest that the latter may be no more

than a subspecies of *agilis*, a taxonomic category not entertained in this report.

SPECIMENS EXAMINED—7 (FMNH). BRAZIL: *Rio de Janeiro*, Teresopolis, 1; *Santa Catarina*, 1; *São Paulo*, Boa Vista, 1; Ilha São Sebastião, 2 (in alcohol); Primeiro Morro, 2 [Brazil: several pouch young and juveniles].

Gracilinanus perijae, new species (figs. 6, 7, 9, 16)

Marmosa marica Handley and Gordon (part, not Thomas), 1979, p. 68—COLOMBIA: *La Guajira* (Las Marimondas, Serranía de Perijá).

HOLOTYPE—Adult male, skin and skull, National Museum of Natural History No. 280881; collected 10 March 1943, by Philip Hershkovitz, original No. 1826.

TYPE LOCALITY—Las Marimondas, the site of a former coffee plantation, eastern slope Serranía de Perijá, Cordillera Oriental de los Andes, north of and above Fonseca at the time in the department of Magdalena, now incorporated into the department of La Guajira, 1450 m.

DISTRIBUTION (fig. 1)—Known only from type locality but the geographic range must include the forested western slopes of the Serranía de Perijá in the drainage basins of the Ríos Cesar and Ranchería on the Colombian side, and the eastern slopes across the divide (1200–1600 m) in the Lake Maracaibo basin of Zulia, Venezuela; northward the Serranía loses altitude before disappearing in the arid scrub savanna of La Guajira; southward

the Serranía gains altitude and joins with the Venezuelan Cordillera de Mérida to continue as the Cordillera Oriental, where suitable habitats for the species may exist.

ETYMOLOGY—Name derived from the Serranía de Perijá, the northernmost spur of the Cordillera Oriental de los Andes in Colombia.

CHARACTERS—**External**—Size, general morphology, and coloration as in other species of the *G. agilis* group; pelage of upper parts and sides slightly crinkly, coloration ochraceous, underparts pale buff, the plumbeous basal portion of the hairs showing through; upper surface of cheirida grayish; blackish eye ring prominent with band extending alongside of muzzle to nose tip; tail brownish above, slightly paler and faintly blotched beneath, the median interscutular hair brownish, laterals grayish, hairs of underside longer, grayish; caudal scales annular; manual claws weak barely extending to tips of terminal phalanges, of toes more robust, recurved, extending to tips.

Cranial—Dorsal outline of skull markedly flat, the braincase little inflated with supraoccipital bone inclined slightly forward, the exoccipital portion visible viewed from above, its axis relative to the basicranial horizontal directed straight back; supraorbital borders nearly parallel-sided with minimal divergence caudad; temporal ridges faint and without indication of postorbital processes or points; bullar process of alisphenoid with antero-medial strut bridging foramen ovale; palate perforated as usual for the genus.

Dental—Fifth upper incisor largest, second slightly smaller, third and fourth intermediate in size; canine well developed; second upper premolar moderately larger than third, both teeth with inner and outer cingula complete.

MEASUREMENTS—See tables 5 and 7.

COMPARISONS—Externally similar to members of the *G. agilis* group except blackish eye ring strongly defined with broad blackish band extending from outer canthus of eye to tip of nasals, a marking shared with *G. dryas* and perhaps some individuals of *G. agilis*. Cranially distinguished from congeners by the low braincase, forward slanting supraoccipital region and exposure of exoccipitals viewed from dorsal surface of skull, its horizontal axis directed straight back; superior postorbital borders more or less parallel-sided, a trait matched by few individuals of *G. agilis*, a species in which incipient postorbital processes or points are present, the braincase dorsally convex.

Nearest geographic ally, *G. marica* of the Cordillera de Mérida, and likewise a denizen of coffee

plantations, differs by poorly defined eye ring, blackish rostral band incomplete or absent, superior postorbital borders slightly divergent, width between temporal ridges at frontoparietal suture border greater, braincase rounded, supraoccipital region inflated, foramen magnum pointed more nearly downward than backward, canines smaller. Measurements (table 7) reveal the morphometric differences between *Gracilinanus perijae* and *G. marica*.

REMARKS—The paratopotype, also a male, collected at the same time (10 March 1943, PH 1831) is quite like the holotype externally; its skull, however, is shattered. The few measurements taken of disassociated parts agree with those of the holotype (tables 5, 7).

The two specimens of *Gracilinanus perijae* were taken at the base of coffee trees in snap traps that also captured *Marmosa robinsoni*, *Micoureus cinereus*, and eight or nine species of sigmodontine rodents, including two species of arboreal oryzomyines and one of *Rhipidomys*. The bait was ripe plantain and peanut butter. Didelphoids are not attracted to manioc, corn, or rice. On the steeply graded slopes of the coffee plantation where most trapping for small mammals was done, canopies of coffee trees at one level above ground are at the same level as the bases of the next higher row of trees. The trees with their trailing vinelike fruit-bearing branches were themselves overhung by vines from the much taller shade trees. The tangle of crisscrossing branches and intertwining vines provides concealed passages from canopy to ground level for small foraging arboreal mammals.

Judged by the catch from traps on the ground, the least captured *Gracilinanus perijae* is most arboreal of the three species of mouse opossums taken in the coffee plantation. *Marmosa robinsoni*, the more frequently captured, is least arboreal or descends more frequently.

SPECIMENS EXAMINED—2 (USNM). COLOMBIA: *La Goajira* (Las Marimondas), holotype and paratopotype.

Gracilinanus sp. (new species)

SPECIMEN EXAMINED—Juvenal female, body in alcohol, skull removed, University of Kansas Museum of Natural History no. 135097; collected 8 August 1970 by J. P. Lynch, original no. 7814.

LOCALITY—Las Palmas, junction Highways 30 and 28, western slope Western Andes, Pichincha, Ecuador, 920 m.

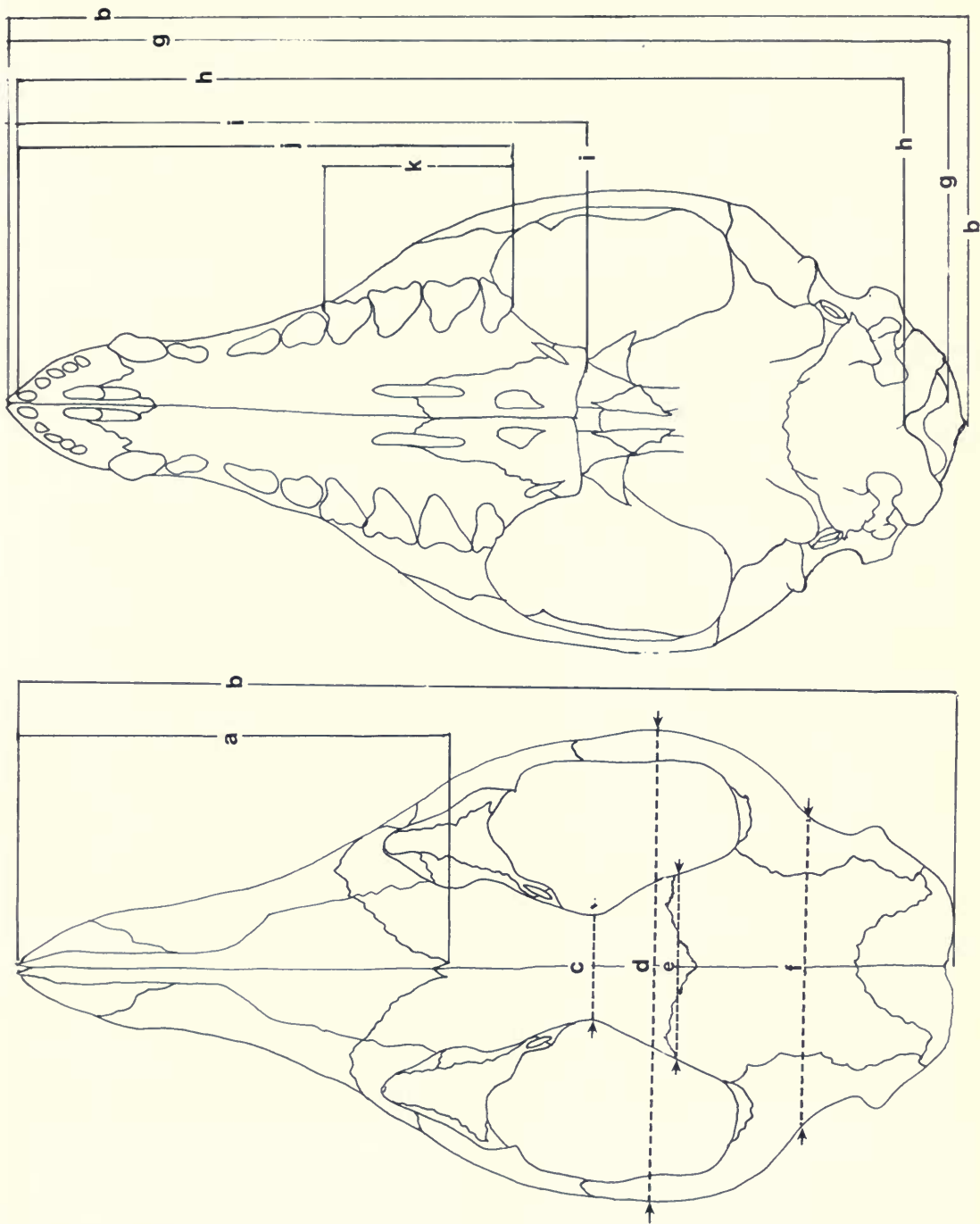


FIG. 17. Outlines of a didelphoid skull; dorsal and palatal aspects showing cranial and dental measurements used in text: a, nasals, greatest length; b, skull, greatest length; c, least interorbital breadth or postorbital constriction; d, zygomatic breadth; e, postorbital width; f, braincase, greatest width; g, condylobasal length; h, basal length of skull; i, palatal length; j, length between first incisor and last molar (i^1-i^5); k, length molar row (m^2-5).

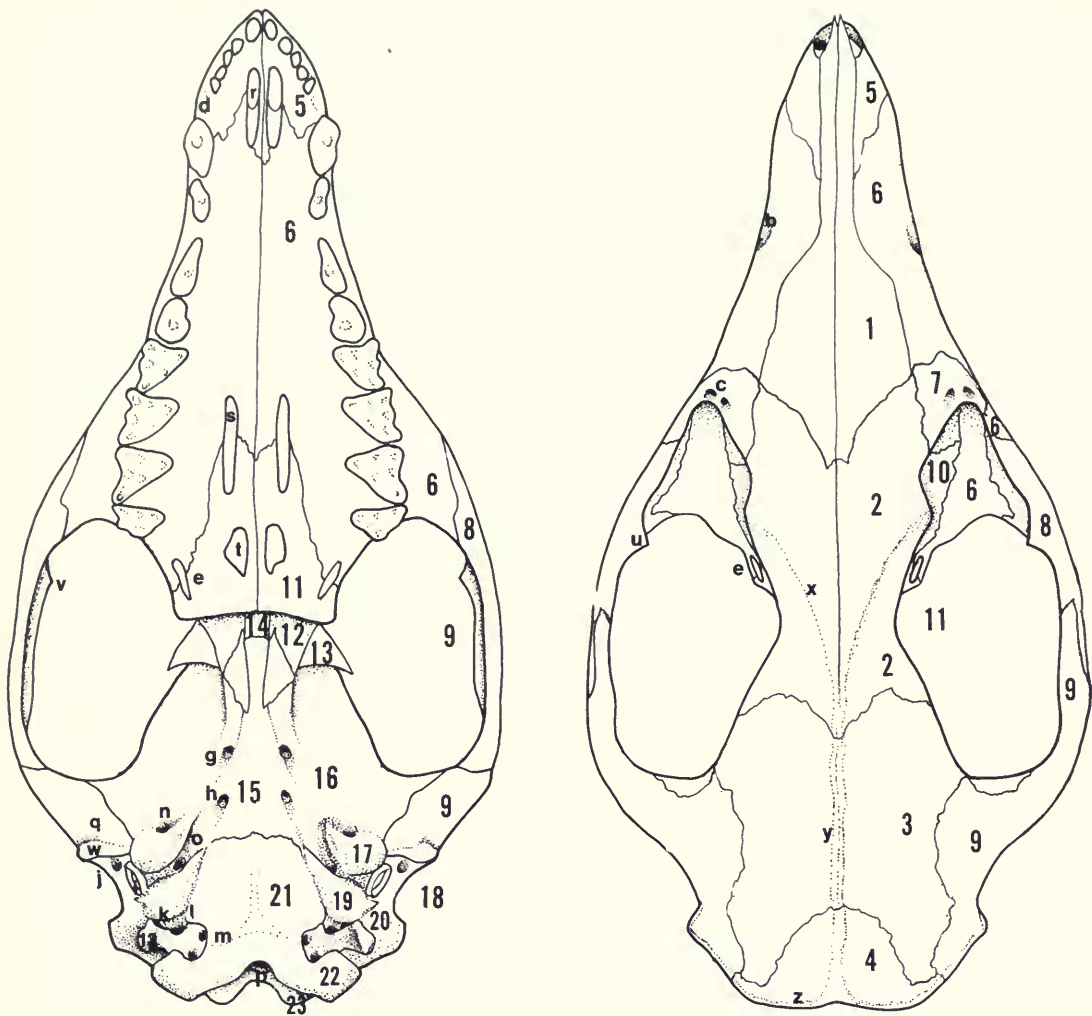


FIG. 18. Composite didelphoid skull; ventral and dorsal aspects showing topographic features. See text for explanation of symbols.

DISTRIBUTION (fig. 1)—Known only from the one locality.

CHARACTERS—External—Upper parts tawny, underparts white, with bright orange lateral band between; dark brown eye ring broad, extending as band to anterior ear base; tail dark brown, scales annular; palmar and plantar interdigital pads separate; intertubercular surface granular; manual claws fine, hardly extending to digital tips, of pes recurved extending to or slightly beyond digital tips.

Cranial—Pronounced supraorbital ridges or beading divergent across frontals, but not to parietals; braincase rounded, the parietals and supraoccipital well inflated; nasals with usual flare

at maxillofrontal suture; tympanic wing of alisphenoid bone half ossified, ectotympanic bone completely exposed; elongate maxillopalatine vacuities partially ossified; maxillary or lateral vacuities absent; posteromedial or palatine vacuities absent; posterolateral vacuities or foramina damaged.

Dental—Upper incisors 1–4 subequal, i^5 largest, cingula obsolete; deciduous $m1$ little worn, $m3$ newly erupted, $m4-5$ unerupted.

MEASUREMENTS (in mm)—H&B, 80; T, 110; hind foot, 18; ear from notch, 16; GSL, 26.9; zygomatic breadth, 14.0; interorbital width, 8.1; postorbital width, 8.1; braincase width, 11.5; nasal length, 9.8; $i-m^3$, 12.5; m^{2-3} , 4.0.

COMPARISONS—The juvenal *Gracilinanus* sp. is

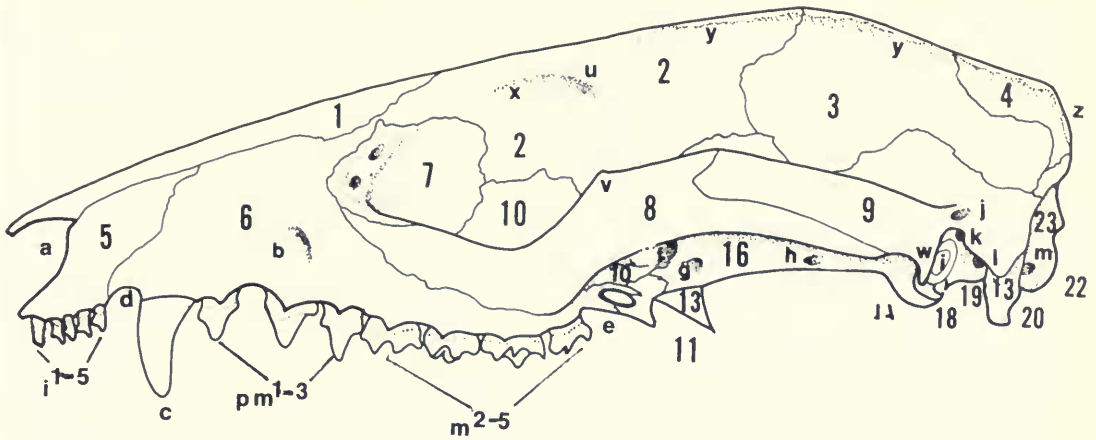


FIG. 19. Composite didelphid skull, left side. See text for names of topographic features of cranium.

Explanation of symbols 1–23 and a–z in figures 18 and 19.

Bones

1. nasal
2. frontal
3. parietal
4. supraoccipital
5. premaxillary
6. maxillary
7. lacrymal
8. jugal, zygomatic
9. squamosal, temporal
10. sphenoid (includes orbitosphenoid, alisphenoid, presphenoid, basisphenoid, pterygoid)
11. palatine
12. orbitosphenoid
13. mastoid (paroccipital) process
14. presphenoid
15. basisphenoid
16. alisphenoid
17. alisphenoidal wing of auditory bulla
18. ectotympanic
19. periotic wing of auditory bulla
20. mastoid (temporal)
21. basioccipital
22. occipital condyle
23. exoccipital

Foramina, Fissures, Processes, Fossae, and Crests

- a. external nares
- b. infraorbital foramen
- c. lacrymal foramina or canal
- d. canine fossa
- e. posterolateral vacuity or foramen
- f. sphenorbital fissure
- g. foramen rotundum
- h. foramen ovale
- i. tympanic membrane and auditory meatus
- j. postglenoid foramen
- k. stylomastoid foramen
- l. jugular foramen
- m. hypoglossal foramen and or condylar foramen
- n. carotid foramen or canal
- o. anterior lacerate foramen or petrotympanic fissure
- p. foramen magnum
- q. glenoid fossa
- r. premaxillary vacuity or incisive foramen
- s. maxillopalatine or mesolateral vacuity
- t. posteromedial or palatine vacuity
- u. postorbital process
- v. ascending postorbital (zygomatic) process
- w. postglenoid process
- x. temporal ridge
- y. sagittal crest
- z. lambdoidal crest

most nearly like adult *Gracilinanus kalinowskii* in external characters and large braincase but differs in absence of posteromedial vacuities and presence of well-developed supraorbital ridges; distinguished from members of the *G. agilis* group mainly by absence of posteromedial palatal vacuities, divergent supraorbital ridges, absence of supraorbital process, and greatly inflated braincase.

REMARKS—This specimen is the first of the genus recorded for Ecuador. The young mouse opossum from Alejandria, near Baeza, Napo, recorded

by Lönnberg (1921, p. 70) as *Marmosa cf. marica*, was identified by Tate (1933, p. 178) as *Marmosops cauae*.

On the label of the *Gracilinanus* sp. he collected, Dr. Lynch wrote "sitting on herbs, 1 m above ground in open area by nite."

This paper was being prepared for publication when the young gracile opossum was brought to me for identification by Dr. Robert M. Timm of the University of Kansas. To my dismay, the specimen appeared to represent still another new spe-

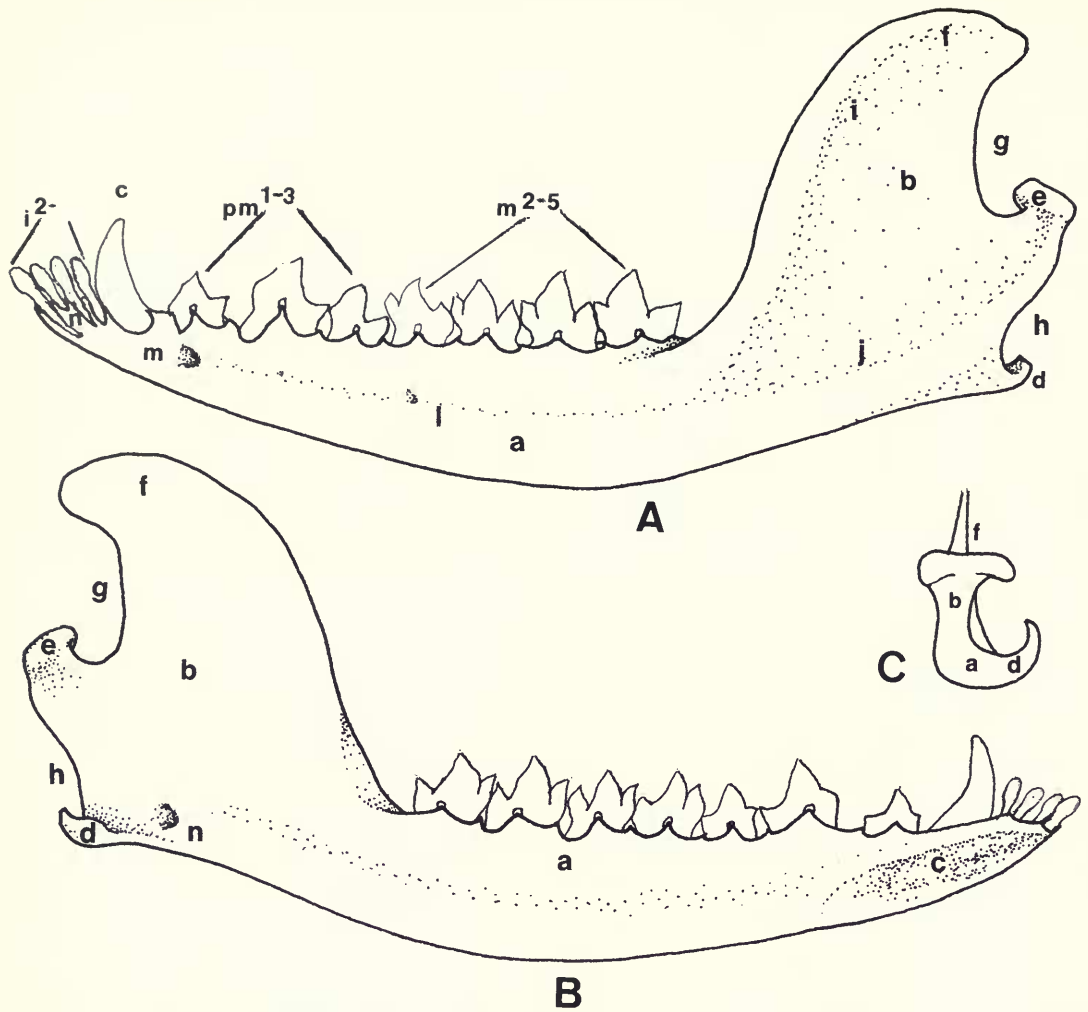


FIG. 20. *Mandible*. **A**, lateral surface; **B**, medial surface; **C**, posterior view. **a**, horizontal ramus; **b**, ascending ramus, and masseteric fossa; **c**, symphysis; **d**, angular process; **e**, condyloid process; **f**, coronoid process; **g**, foramen rotundum; **h**, inferior or lunate notch; **i**, superior masseteric line; **j**, inferior masseteric line; **k**, mylohyoid line; **l**, horizontal masseteric line; **m**, mental foramen; **n**, mandibular foramen.

cies. I was relieved, however, to find it much too young for a formal description, the incorporation of which would have required extensive reorganization of this paper. The present description and comparisons are intended to place on record a species that otherwise might be overlooked.

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Zoological Museum; and the National Museum of Natural History, Smithsonian Institution, Washington, D.C., for the loan of specimens used in this study, and particularly to Dr. Charles O. Handley, Jr., of the latter institution for valuable information regarding holotypes not seen by me; to Dr. Robert M. Timm of the University of Kansas for bringing to my attention the young gracile opossum from Ecuador described herein as *Gracilonomys* sp.; to Research Associate Barbara E. Brown for unstinted assistance; to Technical Assistant Tamara Hamlish for computerization of the manuscript; and to staff artist Zorica Dabich and freelance artists Malena Somoza and Kang Mu for the drawings. For the photographic prints, my spe-

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Appendix 1: Alphabetic List of *Gracilinanus* Collecting Localities

The localities are of specimens examined, type localities, and others mentioned in text including the synonymies. Numbers in parentheses identify localities in the gazetteer (Appendix 2) and their position on the map (fig. 1).

Aceramarca (Río); La Paz, Bolivia (24)
Albarregas (Río); Mérida, Venezuela (10)
alto = upper part, branch, or head of a river
Alto Parnahyba; Maranhão, Brazil (36)
Aranguá (= Araranguá) (66)
Araranguá; Santa Catarina, Brazil (66)
arroyo = stream or river
Balzón (Lago); Bolivia (not located)
Bella Vista; Amazonas, Peru (18)
Betania, Junín; Táchira, Venezuela (12)
Blumenau; Santa Catarina, Brazil (65)
Boa Vista, Río Ipiranga, São Paulo, Brazil (not plotted, see gazetteer in Appendix 2)
Bogotá (Boquerón San Francisco); Cundinamarca, Colombia (14)
Bopicuá (Arroyo); Río Negro, Uruguay (not located)
Bopicuá, Río Uruguay: Río Negro, Uruguay (not located)
boquerón = wide mouth of mountain valley
Brasília; Distrito Federal, Brazil (45)
Brasília, Fundación Zoológica-Botánica; Distrito Federal, Brazil (43)
brazo = fluvial branch
Brazo Largo, Delta del Paraná; Entre Ríos, Argentina (77)
Brumado; Minas Gerais, Brazil (49)
Buenavista; Santa Cruz; Bolivia (27)
Buena Vista; Táchira, Venezuela (11)
cafetal = coffee orchard or plantation
Cafetal de Mérida; Mérida, Venezuela (10)
Cafetal de Milla; Mérida, Venezuela (10)
Cafetales de Mérida; Mérida, Venezuela (10)
Campana; Buenos Aires, Argentina (80)
Cana Brava, Nova Roma; Goiás, Brazil (41)
Chanchamayo; Junín, Peru (20)
Cocos; Maranhão, Brazil (35)
Codajás, Amazonas, Brazil (33a)
Colonia Nueva Italia, Villeta; Chaco, Paraguay (72)
Concepción; Chaco, Paraguay (71)
Crato; Ceará, Brazil (40)
Cristalina; Goiás, Brazil (42)
Culata; Mérida, Venezuela (8)
Ecological Reserve, Instituto Brasileira de Geografia e Estatística; Distrito Federal; Brazil (45)
El = The, masculine article of place name

El Junquito; Distrito Federal, Venezuela (3)
El Limón, Hacienda; Distrito Federal, Venezuela (3)
fazenda = farm (Portuguese)
Fazenda Agua Limpá; Distrito Federal, Brazil (45)
Fazenda Esmeralda, Rio Casca; Minas Gerais, Brazil (not located)
Fazenda Montes Claras; Minas Gerais, Brazil
Franca; São Paulo, Brazil (54)
Fray Bentos-Puerto Ungué; Río Negro, Uruguay (70)
Guahiba (Ilha); Rio Grande do Sul, Brazil (68)
Guahyba; Rio Grande do Sul, Brazil (68)
hacienda = farm (Spanish)
Hacienda Cadena, Marcapata; Cuzco, Peru (22)
hato = hut; shelter; cluster of huts
Humboldt; Santa Catarina, Brazil (63)
Ibiapaba; Ceará, Brazil (38)
Igarapé Grande, Amazonas, Brazil (not plotted)
ilha = island (Portuguese)
Ilha Grande; Rio de Janeiro, Brazil (53)
Ilha São Sebastião, São Paulo, Brazil (60)
Ilha Vitoria; São Paulo, Brazil (58)
Ipu; Ceará, Brazil (37)
isla = island (Spanish)
Isla Roble, Delta del Paraná; Buenos Aires, Argentina (78)
Itapé Camp; Chaco, Paraguay (75)
Itapocu (Rio); Santa Catarina, Brazil (64)
Ituverava; São Paulo, Brazil (55)
Jaboticabal (= Jabuticabal); São Paulo, Brazil (56)
Joinville; Santa Catarina, Brazil (63)
Jua; Ceará, Brazil (39)
Km 50 Manaus-Itacoatiara RR; Amazonas, Brazil (33a)
La = The, feminine article of place name
lago = lake (Spanish)
lagôa = lake (Portuguese)
Lagôa Santa; Minas Gerais, Brazil (50)
La Mucay; Mérida, Venezuela (10)
Las = The, feminine plural article of place name
La Selva; Bogotá; Cundinamarca, Colombia (14)
Las Marimondas; Magdalena, Colombia (13)
Las Palmas; Chaco, Argentina (84)
Las Palmas; Pichincha, Ecuador (17)
llano = plain, savanna
Llano de Mérida; Mérida, Venezuela (10)
Los = The, masculine plural article of place name
Los Venados; Distrito Federal, Venezuela (3)
mata = bush; forest; wooded area
Mata de Bejuco, Hato; Monagas, Venezuela (1)
Mérida; Mérida, Venezuela (10)
Misisí, Hacienda; Trujillo, Venezuela (6)
montaña = extensive forest

monte = local forest; wooded area
 “Montes de la Sierra”; Mérida, Venezuela (10)
 Nueva Italia (Colonia), Villeta; Chaco, Paragua (72)
 Pago del Tigre; Formosa, Argentina (82)
 Palmeira; Paraná, Brazil (62)
 Palomotillas (Río), Buenavista; Santa Cruz, Bolivia (28)
 Pará (= Belém); Pará, Brazil (34)
 parque = park
 Parque Nacional de Brasília; Distrito Federal, Brazil (44)
 Pedregosa; Mérida, Venezuela (9)
 Perus; São Paulo, Brazil (59)
 pico = peak, mountain peak
 Pico Ávila; Distrito Federal, Venezuela (3)
 Pilagá (Riacho); Formosa, Argentina (83)
 Piracicaba; São Paulo, Brazil (57)
 Pitiguaya, Río Unduavi; Yungas, La Paz, Bolivia (25)
 Poconé; Mato Grosso, Brazil (47)
 Pôrto Real; Rio de Janeiro, Brazil (53)
 pozo = well; water hole (Spanish)
 Pozo del Tigre, Patino; Formosa, Argentina (82)
 Primeiro Morro, São Paulo, Brazil (not plotted, see gazetteer in Appendix 2)
 puerto = port (Spanish)
 Puerto Libertad (= Bemberg), Iguazú, Río Uruguay-í; Misiones, Argentina (77)
 Puerto Suárez, Sara; Santa Cruz, Bolivia (30)
 Rancho Grande, Estación Biológica; Aragua, Venezuela (4)
 Reyes, Río Beni, Beni, Bolivia (not plotted)
 riacho = stream, small river or tributary
 Riacho Pilagá; Formosa, Argentina (83)
 rio = river (Portuguese)
 río = river (Spanish)
 Rio de Janeiro; Rio de Janeiro, Brazil (53)
 Rio Doce State Park; Minas Gerais, Brazil (47)
 Sajama, Mt.; Oruro, Bolivia (26)
 salto = water falls, cataract
 San or Santo = Saint, masculine prefix of place name (Spanish)
 San Joaquín; Beni, Bolivia (23)
 San Juan de Arama; Meta, Colombia (15)
 Santa = Saint, feminine prefix of place name
 Santarém; Pará, Brazil (33b)
 Santiago, Chiquitos; Santa Cruz, Bolivia (29)
 São = Saint, masculine prefix of place name (Portuguese)
 São Bento; Goias, Brazil (not located)
 São João da Serra do Norte; Mato Grosso, Brazil (48)
 São Lourenço; Rio Grande do Sul, Brazil (69)

São Sebastião (Ilha); São Paulo, Brazil (60)
 Sapucay; Chaco, Paraguay (73)
 Sepotuba, Salto do; Mato Grosso, Brazil (46)
 Tabay; Mérida, Venezuela (10)
 Tablada; Tarija, Bolivia (32)
 Taquara; Rio Grande do Sul, Brazil (67)
 Teresopolis; Rio de Janeiro, Brazil (52)
 Teresopolis; Rio de Janeiro, Brazil (52)
 Tingo María, Río Huallaga; Huánuco, Peru (19)
 Trujillo; Trujillo, Venezuela (6)
 Turumiquire, Mt.; Sucre, Venezuela (2)
 Uchisera; Mérida, Venezuela (7)
 Unguía; Chocó, Colombia (16)
 Urama; Falcón, Venezuela (5)
 “V. Clarrica” (Tate, 1933, p. 194); probably = Villa Rica, Chaco, Paraguay (74)
 Villa Montes; Tarija, Bolivia (31)
 Villa Rica; Chaco, Paraguay (74)
 Villeta (see Nueva Italia) (72)
 Zarate, Arroyo Nacurutu; Buenos Aires, Argentina (79)

Appendix 2: Gazetteer of *Gracilinanus* Collecting Localities

Venezuela

Monagas

1. Mata de Bejuco, Hato (= hut, shelter), 09°19'N, 62°56'W, 18 m; A. Tuttle and R. Pine, April 1966, June 1968 (*Gracilinanus marica*).

Sucre

2. Turumiquire, Mt., 10°07'N, 63°52'W, 200 m; E. R. Blake, April 1932 (*Gracilinanus marica*).

Distrito Federal

3. El Junquito, 10°28'N, 67°05'W, 1900 m (*Gracilinanus marica*).
3. Los Venados, 10°32'N, 66°54'W, 1400–1739 m, 1600 m; M. Tuttle, A. Tuttle, N. E. Peterson, Flanigan, G. O. Handley, Jr., V. J. Tipton, and Young, July, August 1965 (*Gracilinanus marica*).
3. El Limón (Hacienda), 10°28'N, 67°17'W, 600–1400 m.

3. Pico Ávila (= Hotel Humboldt and vicinity) 10°33'N, 66°52'W, 1982–2288 m; M. Tuttle, A. Tuttle, and C. O. Handley, Jr., August 1956 (*Gracilinanus marica*).

Aragua

4. Rancho Grande, Estación Biológica, 10°21'N, 67°41'W, 1100 m (*Gracilinanus marica*).

Falcón

5. Urama, 10°37'N, 68°24'W, 25–60 m; M. Tuttle and A. Tuttle, October, November 1965; March 1966 (*Gracilinanus marica*).

Trujillo

6. Trujillo, 13–15 km E, 09°21'N, 70°17'W (*Gracilinanus dryas*).
6. Misísí, 09°21'N, 70°18'W; M. E. Peterson and Parish, January 1966 (*Gracilinanus dryas*).

Mérida

7. Uchisera, Cordillera de Mérida, 09°00'N, 71°00'W, 3000 m (*Gracilinanus dryas*).
8. Culata, Cordillera de Mérida, 08°50'N, 71°00'W, 4000 m; S. Briceño Gabaldón (*Gracilinanus dryas*).
9. Pedregosa, 08°37'N, 71°42'W, 1600 m (*Gracilinanus marica*).
10. Mérida, State Capitol, 08°36'N, 41°08'W, 1630 m; S. Briceño Gabaldón (*Gracilinanus marica*; *G. dryas*).
10. Mérida, Cafetales de, 08°36'N, 71°08'W, 1640 m; S. Briceño Gabaldón (*Gracilinanus dryas*; *G. marica*).
10. Mérida, Cafetos de (see Mérida, Cafetales); S. Briceño Gabaldón.
10. Milla, Cafetal de (see Mérida, Cafetales); S. Briceño Gabaldón (*Gracilinanus marica*; *G. dryas*).
10. Montes de la Sierra, 3000 m (see Mérida) (*Gracilinanus dryas*).
10. Albarregas, Río, upper Río Chama, 08°31'N, 71°09'W, 1630 m; S. Briceño Gabaldón, January 1897 (*Gracilinanus marica*, type locality).

10. Llano de Mérida, 08°00'N, 71°10'W; S. Briceño Gabaldón (*Gracilinanus marica*).
10. La Mucay, 5 km E Tabay, 2400 m (see Tabay) (*Gracilinanus dryas*).
10. Tabay, Parque Nacional de la Sierra Nevada, 08°38'N, 71°04'W, 1700 m; N. E. Peterson, Parrish, and V. J. Tipton, March, April 1966 (*Gracilinanus dryas*).

Táchira

11. Buena Vista, near Páramo de Tamá, 07°54'N, 71°59'W, 2400 m; N. E. Peterson, F. P. Brown, and J. O. Matson, March 1968 (*Gracilinanus dryas*).
12. Betania, Junín, 07°27'N, 72°26'W, 2250 m (*Gracilinanus dryas*).

Colombia

La Goajira

13. Las Marimondas, Sierra de Perijá, 10°52'N, 72°43'W, 1450 m; P. Hershkovitz, March 1943 (*Gracilinanus perijae*).

Cundinamarca

14. Bogotá, Boquerón San Francisco, 04°36'N, 74°05'W, 3000 m; P. Hershkovitz, May 1952 (*Gracilinanus dryas*).
14. La Selva, Bogotá (see Bogotá) (*Gracilinanus marica*).

Meta

15. San Juan de Arama, Sierra de la Macarena, 03°18'N, 73°53'W, 396 m; K. von Sneidern, April 1957 (*Gracilinanus longicaudus*, type locality).

Chocó

16. Unguía, 08°01'N, 77°04'W, near sea level; P. Hershkovitz, April 1950 (*Gracilinanus agilis*).

Ecuador

Pichincha

17. Las Palmas at junction of Highways 30 and 28, western slope of Cordillera Occidental, 920 m. Collected 8 August 1970, by J. P. Lynch. In the Ornithological Gazetteer of Ecuador (Museum of Comparative Zoology, Harvard University), Las Palmas is ca 50 km WSW of Quito, ca 25 km ESE of Santo Domingo de los Colorados; 0013S/7830W.

Peru

Amazonas

18. Bella Vista, Río Marañón, right bank, 05°30'S, 78°40'W, 300 m (*Gracilinanus agilis*).

Huánuco

19. Tingo María, 09°08'S, 75°57'W, 600 m; R. W. Hendee, January 1927 (*Gracilinanus agilis*; type locality of *Marmosa agilis peruana* Tate).

Junín

20. Chanchamayo, 11°10'S, 75°20'W, 1100 m; J. M. Schunke, October 1948 (*Gracilinanus kalinowskii*).
(21.) Deleted.

Cuzco

22. Hacienda Cadena, Marcapata, 13°20'S, 70°46'W, 890 m; C. Kalinowski, June 1958 (*Gracilinanus kalinowskii*, type locality).

Bolivia

Beni

23. San Joaquín, 13°04'S, 64°49'W; M. C. Kuns, July 1964 (*Gracilinanus agilis*).
— Reyes, Río Beni, 14°19'S, 67°23'W; A. M. Olalla, December 1937 (*Gracilinanus agilis*). Record received too late to plot on map.

La Paz

24. Aceramarca (= Aceramarca), Río, tributary of Río Unduavi, 16°18'S, 67°53'W, 3275 m; G. H. H. Tate, May 1933 (*Gracilinanus aceramarcae*, type locality).
25. Pitiguaya, Río Unduavi, Yungas, 16°35'S, 67°32'W, 1800 m; G. H. H. Tate, May 1926 (*agilis*; type locality of *Marmosa unduaviensis* Tate).

Oruro

26. Sajama, Mt., 18°07'S, 69°00'W, 4350 m; R. Steinbach, November 1941 (*Gracilinanus agilis*).

Santa Cruz

27. Buenavista, upper Río Yapacani, 17°27'S, 63°21'W, 900 m; J. Steinbach, March 1916 (*Gracilinanus agilis*; type locality of *Marmosa agilis buenavistae* Tate).
28. Palometitlas, Río, Buenavista, 17°36'S, 63°37'W (*Gracilinanus agilis*).
29. Santiago, Chiquitos, 18°19'S, 59°34'W, 730 m; R. Steinbach, February 1973 (*Gracilinanus agilis*).
30. Puerto Suárez, Sara, 18°57'S, 57°51'W, 145 m (*Gracilinanus agilis*).

Tarija

31. Villa Montes, 21°15'S, 62°30'W, 500 m (*Gracilinanus agilis*).
32. Tablada, 21°23'S, 64°47'W, 2000 m; E. Budin, December 1924 (*Gracilinanus agilis*).

Not Located

- Balzón, Lago (*Gracilinanus agilis*).

Brazil

Amazonas

- 33a. Km 50, Manaus–Itacoatiara RR, 03°09'S, 60°43'W, 100–200 m; C. Elias, January–February 1961 (*Gracilinanus emiliae*).

- 33a. Codajás, Rio Solimões, 03°50'S, 62°05'W, 35 m; A. M. Olalla, December 1935 (*Gracilinanus emiliae*).
— Igarapé Grande, upper Rio Juruá, 06°43'S, 70°26'W, ca. 150 m; A. M. Olalla, 1936 (*Gracilinanus emiliae*). Record received too late to plot on map (cf. Patterson, 1992).

Pará

- 33b. Santarém, mouth Rio Tapajóz, 02°26'S, 54°42'W, 51 m (*Gracilinanus emiliae*).
34. Pará (= Belém), 01°27'S, 48°29'W, near sea level; E. Snethlage, February 1909 (*Gracilinanus emiliae*, type locality).

Maranhão

35. Cocos, 04°30'S, 43°50'W, ca. 60 m; E. Snethlage, July 1924 (*Gracilinanus agilis*).
36. Alto Rio Parnahyba, 06°46'S, 43°00'W, 400–600 m; E. Snethlage, July, August 1925 (*Gracilinanus agilis*).

Ceará

37. Ipu, 04°20'S, 40°42'W, 300 m; E. Snethlage, 1910 (*Gracilinanus agilis*, type locality of *Marmosa agilis beatrix* Thomas).
38. Ibiapaba, 05°03'S, 40°55'W, 300 m; E. Snethlage, January 1924 (*Gracilinanus agilis*).
39. Jua, near Iguatú, 06°22'S, 39°18'W, 215 m; R. H. Becker, August 1913 (*Gracilinanus agilis*).
40. Crato, 07°14'S, 39°23'W, 427 m; A. Leitão de Carvalho (*Gracilinanus emiliae*).

Goiás

41. Cana Brava, Nova Roma, 13°40'S, 47°07'W (*Gracilinanus agilis*).
42. Cristalina, 12 km NE, 16°45'S, 47°36'W, 1189 m; M. Mares, J. Braun, and D. Gettinger (*Gracilinanus agilis*).

Distrito Federal

43. Brasília, Fundação Zoologia–Botânica,

- 15°35'S, 47°55'W; P. Hershkovitz, August 1986 (*Gracilinanus agilis*).
44. Parque Nacional de Brasília, 15°35'S, 48°54'W, 700–1300 m; C. R. Alho, L. A. Pereira, and A. C. Paula, January–December 1982 (*Gracilinanus agilis*).
45. Agua Limpa, Fazenda, 15 km SW Brasília, 15°08'S, 47°57'W, 1000 m; L. Nitikman and M. Mares, January–July 1984; M. A. Mares, K. Ernest, and D. Gettinger, August 1983–November 1984; C. Alho, L. A. Pereira, and A. C. Paula, 1986 (*Gracilinanus agilis*).
45. Brasília, 15°56'S, 47°53'W, 1172 m.
45. Reserva Ecologia, Instituto Brasileiro de Geografia e Estatística, 15°59'S, 47°56'W; M. Mares, K. Ernest, and D. Gettinger (*Gracilinanus agilis*).

Mato Grosso

46. Sepotuba, Salto de, Rio Paraguai, 15°55'S, 57°37'W (*Gracilinanus agilis*; one of two type localities of *Marmosa rondoni* Miranda Ribeiro).
47. Poconé, 16°15'S, 56°37'W; M. Mares, J. Braun, and D. Gettinger, between July 1983 and November 1984.
48. São João da Serra do Norte, 16°45'S, 53°03'W (*Gracilinanus agilis*; second of two type localities of *Marmosa rondoni* Miranda Ribeiro).
49. Brumado, 21°07'S, 44°18'W; P. W. Lund (*Gracilinanus agilis*).

Minas Gerais

50. Lagôa Santa, 19°38'S, 48°53'W, 760 m; H. Burmeister (*Gracilinanus agilis*, type locality).
51. Rio Doce State Park, 19°48'–19°29'S, 42°38'–42°28'W; G. da Fonseca and M. Kierulff, October 1986; J. R. Stalling, September 1985–February 1987 (*Gracilinanus microtarsus*).

Rio de Janeiro

52. Teresopolis, 22°26'S, 42°59'W, 950 m; C. C. Sanborn, July 1926; D. E. Davis, May 1942–May 1943 (*Gracilinanus microtarsus*).
52. Teresopolis (see Teresopolis).

53. Rio de Janeiro, 22°54'S, 43°14'W, near sea level (*Gracilinanus microtarsus*).
53. Pôrto Real, 22°25'S, 44°20'W, near sea level (*Gracilinanus microtarsus*).
53. Ilha Grande, 23°09'S, 44°30'W, near sea level; E. Garbe, 1905 (*Gracilinanus microtarsus*).

São Paulo

54. Franca, 20°32'S, 47°24'W, 997 m (*Gracilinanus microtarsus*).
55. Ituverava, 20°20'S, 47°47'W, 605 m (*Gracilinanus microtarsus*).
56. Jaboticabal, 21°16'S, 48°19'W, 605 m; J. Lima, 1897 (*Gracilinanus microtarsus*).
57. Piracicaba, 22°43'S, 47°38'W, 548 m (*Gracilinanus microtarsus*).
58. Ipanema (= Bacaetava), 23°26'S, 47°36'W, 600 m; J. Natterer, June 1819, October 1821 (*Gracilinanus microtarsus*).
58. Ypanema (see Ipanema).
59. Perus, São Paulo, 23°25'S, 46°45'W, near sea level (*Gracilinanus microtarsus*).
60. São Sebastião, 23°48'S, 45°25'W, near sea level (*Gracilinanus microtarsus*).
61. Ilha Vitoria, 23°50'S, 45°00'W, near sea level; Gunther, 1906, 1907 (*Gracilinanus microtarsus*).
- Primeiro Morro, 24°22'S, 47°49'W; A. M. Olalla, August 1960.
- Boa Vista, Río Ipiranga, 24°35'S, 47°38'W; A. M. Olalla, September 1961.

Paraná

62. Palmeira, 25°25'S, 50°00'W, 865 m (*Gracilinanus microtarsus*).

Santa Catarina

63. Humboldt (= Colonia Hansa), ca. 26°S, 49°W (*Gracilinanus microtarsus*; type locality of *Marmosa herhardti* Miranda Ribeiro).
63. Colonia Hansa (see Humboldt).
63. Joinville, 26°18'S, 48°50'W, near sea level (*Gracilinanus microtarsus*).
64. Itapocu (Rio), near, 26°34'S, 48°40'W (*Gracilinanus microtarsus*).
65. Blumenau, 26°56'S, 49°03'W, 22 m (*Gracilinanus microtarsus*).

66. Araranguá, 28°56'S, 49°29'W, 13 m (*Gracilinanus microtarsus*).

Rio Grande do Sul

67. Taquara, 29°39'S, 50°47'W, 29 m (*Gracilinanus microtarsus*).
68. Guahiba, Ilha, 30°06'S, 50°19'W, near sea level; R. Hensel (*Gracilinanus microtarsus*; type locality of *Marmosa microtarsus guahybae* Tate).
68. Guahyba (see Guahiba).
69. São Lourenço, 31°22'S, 51°58'W, near sea level (*Gracilinanus microtarsus*).

Not Located

- São Bento (*Gracilinanus agilis*; type locality of *Marmosa blaseri* Miranda Ribeiro).

Uruguay

Rio Negro

- Bopicuá, Río Uruguay (not located); J. C. González, September 1979 (*Gracilinanus agilis*); J. P. Lescano and J. C. González, March 1976 (*Gracilinanus agilis*).
70. Fray Bentos–Puerto Ungué, Río Uruguay, 33°07'S, 58°19'W; J. C. González, February 1978 (*Gracilinanus agilis*).

Paraguay

Chaco

71. Concepción, 23°20'S, 57°25'W, 175 m (*Gracilinanus agilis*).
72. Colonia Nueva Italia, Villeta, 25°37'S, 57°30'W, 100 m; P. Willem (*Gracilinanus agilis*).
73. Sapucay (= Sapucaí), 25°40'S, 56°55'W, 220 m; W. Foster, September 1903 (*Gracilinanus agilis*; type locality of *Marmosa agilis chacoensis* Tate).
74. Villa Rica, 25°45'S, 56°26'W, 200 m (*Gracilinanus agilis*).
75. Itapé Camp near Sapucay, 25°51'S, 56°38'W, 200 m (*Gracilinanus agilis*).

Argentina

Misiones

76. Puerto Libertad-Iguazú, Río Uruguay, ca 26°30'S, 54°16'W; J. A. Crespo, September 1949 (*Gracilinanus agilis*).

Entre Ríos

77. Brazo Largo, Delta del Paraná, 33°47'S, 58°36'W, near sea level; E. Massoia, A. Fornés, and Torres (*Gracilinanus agilis*).

Buenos Aires

78. Isla Roble, Delta del Paraná, 33°43'S, 59°15'W, near sea level (*Gracilinanus agilis*).
79. Zárate, Arroyo Nacurutú, 34°09'S, 58°59'W; E. del Ponte, March 1949 (*Gracilinanus agilis*).

80. Campana, 35°13'S, 58°54'W; E. Massoia et al., 1964, 1968, 1969, 1970 (*Gracilinanus agilis*).

81. Ingeniero Juárez, 23°54'S, 61°51'W, 100 m; S. Pierotti and O. Budín, August, September 1950 (*Gracilinanus agilis*).

Formosa

82. Pago del Tigre, Patiño, 24°54'S, 60°19'W; A. Fornés, August 1968 (*Gracilinanus agilis*).
83. Riacho Pilagá (= Estancia Linda Vista), 26°05'S, 57°59'W, 100 m; A. Wetmore, August 1920 (*Gracilinanus agilis*; type locality of *Marmosa muscula* Shamel = *Marmosa formosa* Shamel).

Chaco

84. Las Palmas, 27°04'S, 58°42'W (*Gracilinanus agilis*).